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Biological specialization in Darluca filum

PAUL D. KEENER[1]

(WITH PLATE 25)

The genus *Darluca* comprises a comparatively small group of parasitic fungi of the Family Sphaeropsidaceae of the Order Sphaeropsidales of the Class Fungi Imperfecti. It was named in honor of Michel Darluc, a French doctor of medicine. The members of the genus are well known as parasitizing the rust fungi, occurring on a variety of rusts scattered throughout the entire world. The present paper deals with the results of greenhouse cultures of *Darluca filum* (Biv.) Cast. on various rusts. The writer (Keener, 1933) has already reported the results of laboratory studies with pure cultures of this species of *Darluca*.

HISTORICAL

The most common and widely distributed species of the genus is *Darluca filum* which was first described as *Sphaeria filum* by Bivona-Bernardi in the year 1813. In 1823 Fries described the same fungus as *Phoma filum*. The generic name *Darluca* was established by Castagne in 1851, who cited *Sphaeria filum* as the type species. Previous to this time the same fungus had already been sent out from the Castagne herbarium to several European botanists as *Darluca vagans*, so that in reality the generic name was in limited use sometime before the actual founding of the genus. Since the name *Darluca vagans* as used by Castagne previous to 1851, was not published, it cannot be recognized under any system of nomenclature as valid. On the other hand, *Phoma filum* of Fries, in view of its proper publication, does become a synonym of *Darluca filum* (Biv.) Cast.

Darluca filum has been reported on both macro-cyclic and micro-cyclic rusts, and as occurring on the aecial, uredinial, and telial sori, but more commonly on the uredinia. Among the rusts on which this species has been reported, are representatives of such genera as *Aecidium*, *Cerotelium*, *Chrysomyxa*, *Coleosporium*, *Frommea*, *Kuehneola*, *Melampsora*, *Peridermium*, *Phragmidium*, *Pileolaria*, *Puccinia*, *Ravenelia*, *Tranzschelia*, *Uromyces*, *Uromycladium*, and *Uredo*. In addition the author has observed *D. filum* on the rust genera *Gymnoconia* and *Phakopsora*. The examples

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below will give some idea as to the variety of rusts on which this species of *Darluca* has been found. In 1851 Castagne reported *D. filum* (as *D. vagans*) on *Pileolaria Terebinthi*. In 1897 Cobb reported *D. filum* on *Tranzschelia punctata*. In 1906 McAlpine reported *D. filum* on several Australian rusts among which were *Uromycladium simplex*, two species of *Aecidium*, and *Phragmidium Potentillae*. In 1913 it was listed by Lind on *Chrysomyxa Abietis*. In 1920 Adams reported *D. filum* on *Peridermium Peckii* (*Pucciniastrum Myrtilli*) on *Tsuga canadensis* and on *Coleosporium delicatulum* on *Euthamia tenuifolia*. So far as is known, this was the first report of its occurrence on a Gymnosperm rust. In 1929 Moss found *D. filum* on *Melampsora confluens* on *Salix lutea*. In 1930 Sydow (p. 186) reported it on *Ravenelia spinulosa* on *Cassia biflora* in South America. During the same year, Stevens (1930a) reported *D. filum* as occurring on *Uredo Dioscoreae* on *Dioscorea* sp. in Panama. In 1931 Petrak and Ciferri reported the parasite on *Ravenelia Ingae* on *Inga vera*. It has been said by some authors that *D. filum* attacks at least twenty-four percent of the species of the rust genus *Puccinia* and almost as high a percentage of the species of the genus *Uromyces*.

Darluca filum has also been reported in association with fungi other than the Rusts. In 1930 (b) Stevens listed *D. filum* in association with the fungus *Diplodia uredinicola*. Previous to this report, Castagne (1851) had listed *D. filum* (as *D. vagans*) on *Diplodia perpusilla*.

Since the founding of the genus there have been described in the literature approximately twenty-five other species of *Darluca*. Various reports have listed these primarily as rust parasites, although a few species have been listed as occurring directly on phanerogamic hosts, or in association with fungi other than the rusts. For those species recorded as occurring directly on phanerogamic hosts, unassociated with rusts, Clements and Shear (1931) have proposed the creation of the new genus *Darlucis*. Accordingly, the genus *Darluca* would thus be split up into two genera, retaining the name *Darluca* for those species parasitic on rusts.

A perfect stage in the *Darluca* life history has been established under the generic name *Eudarluca* by Spegazzini in 1908. This genus is classed in the Family Sphaeriaceae of the Order Sphaeriales of the Class Ascomycetes. When Spegazzini set up the genus he described *Eudarluca australis* as the type species. In 1910 the same author described *Darluca australis* which apparently he thought was the imperfect stage of *Eudarluca australis* Speg. although an actual connection between the two stages has undoubtedly never been established by cultural methods. So far as can be determined from the literature, there has been only one other species of *Eudarluca* described, namely, *Eudarluca venezuelana*, reported

by Sydow (1930, p. 71) from Venezuela, South America. In the same report, Sydow (1930, p. 186) described an imperfect form, *Darluca venezuelana*, and here again it is apparent that there is merely an assumed connection between the imperfect or *Darluca* stage and the perfect or *Eudarluca* stage. The writer has observed an ascomycete on *Puccinia obscura* on *Juncoides campestre* and on *Puccinia Peckii* on *Carex normalis*, in Pennsylvania, which he believes may be a perfect stage of *Darluca filum*. Inoculations with this fungus as well as with the imperfect forms are herein reported.[2]

Probably the first attempt at culture work with any *Darluca* species was made by Sappin-Trouffy in the year 1896. This worker germinated *Darluca* conidia in contact with rust spores on the surface of water cultures in the laboratory. He observed that upon germination, the conidia sent hyphal strands into the urediniospores and teliospores of the rusts concerned. In an article concerning *Darluca* on *Uromyces caryophyllinus* and on *Puccinia Asparagi*, Blodgett (1907–1908) suggested that the fungus might be cultured by spraying conidial suspensions on rusted carnation and asparagus plants in the greenhouse.

MORPHOLOGY OF THE FUNGUS

During its development in the field, *D. filum* produces small, globose or elongated, black, shiny, fruiting bodies known as pycnidia. These structures vary considerably in size, are slightly beaked, and are sometimes fused at their bases or along the pycnidial wall (Pl. 25, figs. 4, 6, 7). They possess distinct ostiolar openings, through which the spores are exuded in thin, white or grayish, mucilaginous, threads. The ostiolar papillae become somewhat depressed as the pycnidia mature.

The pycnidia occur either singly or in groups, within or upon the rust sorus (Pl. 25, figs. 1–8), and rarely directly on the host plant epidermis. In the latter case, the fungus is probably parasitic on the rust hyphae concealed within the tissues of the host plant.

The spores are produced in great numbers within the pycnidial cavity (Pl. 25, fig. 5). Adams (1920, fig. 4) although not discussing such a process, shows that the conidia are produced singly and acrogenously, at

[2] Isolation No. 11–1 was made from conidia and isolations No. 11–2 and 12–2 from the ascospores of this fungus. Inoculation results with isolations No. 11–1 and 12-2 are herein recorded. The fungus shows all the characteristics of *Darluca filum*, but until further studies have been completed, the author has reserved his opinion as to the exact status of this form. For the present it will suffice to say that isolations No. 11–1 and 12–2 may be looked upon as constituting strains of the common species *D. filum*.

the tips of short pedicel-like hyphal processes sent out from the cells of the pycnidial wall; a single wall cell producing but one hyphal process with a spore at its tip (Pl. 25, figs. 5, 6). Such a method of spore production is not uncommon in certain members of the Order Sphaeropsidales to which *Darluca* belongs. The conidia are 2-celled, sometimes 3-4-celled, hyaline, oblong to fusoid, 10–21×3–7μ, slightly constricted at the septa, and when young possess two apiculate spine-like projections at each end of the spore. These spines tend to disappear as the spores become mature. As a result of this tendency for the older spores to lose their spines, Adams (1920) was led to conclude that there might possibly exist two distinct strains of the parasite; one with spines on the spores and the other lacking such spore structures.

In the generic description published in 1851, Castagne made no mention of spines on the spores of his specimen. So far as can be determined from the literature, the first mention of these structures was by Saccardo in 1884.

OBJECT

The object of this work was to determine whether or not biological specialization exists within the species *Darluca filum*, and if so, the extent to which it occurs. An indication of specialization was secured from the author's previous study of several isolations and their behavior on various laboratory culture media (Keener, 1933)

MATERIALS AND METHODS

Pure cultures of isolations from conidia of *D. filum* as well as from ascospores of the fungus found on *Puccinia obscura* and on *Puccinia Peckii*, were used as a source of spore inoculum with which to conduct the greenhouse cultures. Each isolation was considered a strain and the two terms are hereafter used interchangeably.

The author (Keener, 1933) has already described the methods used in isolating from conidia and ascospores. By the use of these methods, thirteen isolations (11 from conidia and 2 from ascospores), from 11 different rusts (7 of the rust genus *Puccinia* and 4 of the genus *Uromyces*), on 10 different phanerogamic hosts, collected in 3 states, were made. The isolations with their arbitrary pure culture numbers and their sources, are given in the table on the next page.

The culture work conducted in the greenhouse can be conveniently divided into two phases, (1) the culturing of the various rusts on their phanerogamic hosts, and (2) the culturing of the various *Darluca* isolations on these rusts.

Rust cultures. In order to obtain suitable material to be inoculated with *D. filum*, healthy plants had to first be infected with various rusts. To secure rust infections the atomizer, hypodermic syringe, and scalpel methods were employed. The first method proved to be the most satisfactory for the majority of rusts used. For each inoculation, a suspension of

PURE CULTURE NUMBER	SOURCE		
	NAME OF RUST HOST	PHANEROGAMIC HOST	STATE
1	*Puccinia Sorghi*	*Zea Mays*	Pennsylvania
2	*Puccinia poculiformis*	*Phleum pratense*	Pennsylvania
3	*Uromyces Silphii*	*Juncus tenuis*	Pennsylvania
3-B	*Uromyces Silphii*	*Juncus tenuis*	West Virginia
4	*Uromyces fallens*	*Trifolium pratense*	New Jersey
5	*Puccinia hibisciata*	*Muhlenbergia Schreberi*	New Jersey
6	*Puccinia Violae*	*Viola* sp.	New Jersey
7	*Uromyces Polygoni*	*Polygonum aviculare*	Pennsylvania
8	*Uromyces Junci-effusi*	*Juncus effusus*	Pennsylvania
9	*Puccinia Hieracii*	*Leontodon Taraxacum*	Pennsylvania
*11-1	*Puccinia obscura*	*Juncoides campestre*	Pennsylvania
**11-2	*Puccinia obscura*	*Juncoides campestre*	Pennsylvania
**12-2	*Puccinia Peckii*	*Carex normalis*	Pennsylvania

* Isolated from conidia.
** Isolated from ascospores.

urediniospores in distilled water was prepared in the bowl of an atomizer, and was then sprayed onto healthy, potted plants in the greenhouse. Plants so treated were then placed in sand pits and covered with bell jars. The bell jars were removed in from 24 to 48 hours.

In their studies on smut resistance in corn seedlings grown in the greenhouse, Tisdale and Johnston (1926) found that the use of a hypodermic syringe proved to be a highly satisfactory means of inoculation. Inoculations made in this manner were most satisfactory for securing a good distribution of rust sori on both corn and bean plants. In using this method, a suspension of urediniospores in distilled water was drawn up into the tube of a hypodermic syringe, and was then injected into healthy plants, at the ground level. When this method is used, bell jars can be dispensed with. The rust infections which resulted spread to even the uppermost leaves of the host plants.

In the majority of cases, urediniospores were the inoculum used. In the case of *Puccinia Malvacearum* the inoculum consisted necessarily of basidiospores. To secure infections with this rust, heavily rusted hollyhock leaves were brought in from the field and were supported on wire

gauzes over healthy, potted plants in the greenhouse. The inoculated plants were then covered with bell jars as before.

In a few instances, such as for *Kuehneola Uredinis* on *Rubus alleghenensis*, *Puccinia Anemones-virginianae* on *Anemone virginiana*, *Puccinia Circaeae* on *Circaea alpina*, and *Uromyces verruculosus* on *Lychnis alba*, it was necessary to depend on plants that had become naturally rusted under field conditions. Such plants were dug up, were transplanted in separate pots in the greenhouse and allowed to stand for two weeks, in order to be certain that no stray infections of *Darluca* from the field were present. A final examination was given these plants before inoculating them with the various *Darluca* isolations.

Darluca cultures. In making inoculations onto rusts with the various isolations of *D. filum*, a suspension of conidia from pure cultures was prepared, and an atomizer was then employed to spray the suspensions on rusted plants in the greenhouse. Each time an inoculation was made, a bell jar was placed over the inoculated plant for a period of from 24 to 48 hours. Results of inoculations were observed in from 6 to 9 days after the initial set-up.

After each series of inoculations, bell jars were sterilized by spraying them with a 20% formaldehyde solution. The sand used in the pits was discarded, and the pits themselves sterilized by spraying them with the same percent formaldehyde. Atomizers were sterilized after each inoculation, by submerging them in 70% alcohol for from 12 to 24 hours.

Altogether nineteen rust species representative of five genera were employed as hosts for the isolations of *Darluca*. Among these were two species of the genus *Coleosporium*, one of *Frommea*, one of *Kuehneola*, eleven of *Puccinia*, and four of *Uromyces*. Of these, three were micro-cyclic, while sixteen were macro-cyclic species. In some instances it was impossible to inoculate all nineteen rusts with a given isolation of the parasite. This was due either to insufficient rust material or to the dying off of certain phanerogamic hosts in the greenhouse.

In view of the fact that particular rust species used in this work occur naturally on more than one phanerogamic host, a more complete citation of hosts for such rusts precedes Table 1.

RESULTS

Isolations No. 9 and 11–2 failed to produce sufficient spores with which to conduct greenhouse inoculations.

Table 1 shows the varied reactions of eleven of the thirteen isolations of *D. filum* on the nineteen rust species. Wherever blanks occur, they indicate that no inoculation of the particular strain on the rust species

concerned, was made. In Table 1 the fractions were determined as Ratio = $\frac{\text{Number of rusted leaves inoculated}}{\text{Number of rusted leaves infected}}$. Zeros in the denominators therefore indicate negative inoculation results. The average percentage of infection figures in the last column of the table, show the relative susceptibility of any one of the nineteen rusts to the eleven isolations of the parasite. The lowermost row of average percentage of infection figures, show the relative virulence of any particular isolation on the nineteen rust species. Average percentage of infection was determined as, Average percentage of infection $= \frac{\text{Number of leaves infected}}{\text{Number of leaves inoculated}} \times 100$. The table, therefore, shows the inoculation results not only from a simple positive and negative standpoint, as determined from the ratios, but also from the average percentage of infection standpoint, as determined, from the figures in the last column and the lowermost row.

TABLE 1

*Relative susceptibility of nineteen rusts and relative virulence of eleven isolations of Darluca filum.**

NAME OF RUST HOST	ISOLATION NUMBER											AV. % INF.
	1	2	3	3 B	4	5	6	7	8	11 1	12 2	
Coleosporium Campanulae	3/0		3/0		7/0							0
Coleosporium Solidaginis	5/0	5/0	6/3	9/0	7/0	8/0	4/1	8/0	9/0		4/0	6
Frommea obtusa	6/0	4/3	4/0	2/2	1/1	1/1	2/2	2/0	6/2	2/1	3/2	42
Kuehneola Uredinis	21/10	3/0	5/3	8/0	8/0	18/9	12/0	4/0	10/0	10/0	6/0	21
Puccinia Acetosae	6/4	28/8	9/0	10/0	10/0	10/5	8/3	6/4	4/2			42
Puccinia Anemones-virginianae	3/3	4/4	4/3	4/0	4/4	2/1	5/0	5/0	6/2	3/3	2/0	79
Puccinia Antirrhini	30/6	38/11	12/0	46/11	20/0	21/12	34/13	6/6	19/9	12/10	14/8	34
Puccinia Circaeae	5/5	6/0	3/3	6/3	10/6	7/5	6/0	7/0	6/3	10/5	4/3	47
Puccinia Clematidis	5/4	3/3	4/0	4/0	5/0	5/0	4/0	4/3	12/0	5/1	3/0	20
Puccinia Hieracii	30/10	4/1	10/6	34/0	6/3	14/8	12/0		17/11			31
Puccinia Malvacearum	4/0				7/0			4/0	3/2			11
Puccinia Menthae	21/13	12/0	8/0	18/0	22/0	30/21	15/10	10/0	59/40	44/26	19/14	50
Puccinia poculiformis (1)	10/0	35/23	25/0	27/0	29/11	33/30	28/21	25/0				40
Puccinia poculiformis (2)	3/0	8/0	3/0	8/0	7/0	4/0	3/0	10/0	3/0			0
Puccinia Sorghi	20/12	30/15	25/20	25/5	7/4	23/19	17/11	10/9	21/12	10/6	12/6	60
Uromyces appendiculatus	14/10	10/5	7/0	14/0	7/4	17/5	12/4	10/8	7/4	14/0	11/5	37
Uromyces caryophyllinus	5/0			17/5		9/9			15/7	8/3		44
Uromyces Polygoni	14/11	30/29	10/6	14/8	24/15	12/0	17/13	21/14	42/21	13/0	13/10	60
Uromyces verruculosus	5/0	14/11	34/15	6/0	21/5	11/7	36/0		9/0		20/10	31
Av. Percentage of Infection	42	48	34	13	26	59	36	33	46	42	52	×

* Ratio $= \frac{\text{No. of leaves inoculated}}{\text{No. of leaves infected}}$

Average percentage of infection $= \frac{\text{No. rusted leaves infected}}{\text{No. rusted leaves inoculated}} \times 100.$

In Table 1, *Coleosporium Campanulae* represents the uredinial stage of that rust on *Campanula rapunculoides* and *Coleosporium Solidaginis* the uredinial stage on *Solidago* sp. The host for *Puccinia Clematidis* was *Triticum aestivum*, while *Puccinia poculiformis* (1) had *Phleum pratense* for its host, and *Puccinia poculiformis* (2) was on *Poa compressa*. *Puccinia Hieracii* was used on *Leontodon Taraxacum* and *Puccinia Malvacearum* on *Althaea rosea*. *Puccinia Menthae* was on *Mentha spicata* while *Uromyces Polygoni* was on *Polygonum aviculare*. Golden Bantam sweet corn was employed as the host for *Puccinia Sorghi*, and Early Dawn carnation was used as the host for *Uromyces caryophyllinus*. For *Uromyces appendiculatus* the host was *Phaseolus vulgaris* var. "Kentucky Wonder." *Frommea obtusa* was on *Potentilla canadensis* and *Puccinia Acetosae* was on *Rumex Acetosella*, and *Puccinia Antirrhini* was on *Antirrhinum majus*. Other hosts have been previously mentioned.

DISCUSSION AND CONCLUSIONS

The writer's previous studies (Keener, 1933) of ten isolations of *Darluca filum* on various laboratory media, indicated the presence of six distinct strains of the rust parasite. However, the results of greenhouse cultures with eleven of thirteen isolations herein discussed, show that it is better to consider each isolation a distinct strain of *D. filum*.

In the remarks to follow, several terms are used which it seems advisable to define:

(1) Susceptibility: that quality of a host allowing for a successful attack by the parasite. As herein employed it denotes that quality of the various rust hosts which permitted them to be attacked by the various isolations. The degree of susceptibility of one rust as compared with another under similar conditions may be regarded as relative susceptibility, and may be roughly determined by comparing the average percentage of infection figures in the last column of Table 1.

(2) Virulence: that quality of the parasite which enables it to attack a host successfully. As mentioned herein it is used to denote that quality of the various *Darluca* isolations which enabled them to attack the various rusts. The degree or intensity of virulence of one isolation as compared with another under similar conditions may be looked upon as relative virulence, and in this instance may be determined by comparing the average percentage of infection figures in the bottom row of Table 1.

By the use of previously described methods, 175 inoculations with eleven of the thirteen isolations of *D. filum*, were completed. Of this number 101 or 58% proved to be positive and 74 or 42% gave negative results. Of the 175 inoculations, 149 were made on the 16 macro-cyclic (long-

cycled), and 26 on the 3 micro-cyclic (short-cycled) rust species. Of the 149 inoculations onto the 16 macro-cyclic rusts, 85 or 57% gave positive results and 64 were negative. The 26 inoculations onto the 3 micro-cyclic rusts resulted in 16 or 62% positive and 10 negative trials.

Considering the results from the standpoint of the rusts and also from that of the isolations, it will be noted that there are two possible ways of interpreting the specialization that is shown:

(1) The nineteen rusts varied in their susceptibility to the different isolations. Some rusts were more susceptible than others and some were non-susceptible.

(2) The eleven isolations proved variable in their virulence on the nineteen rusts. Any single isolation was more virulent on some rusts than it was on others.

From the standpoint of susceptibility to all isolations tested, the ratios in Table 1 show that *Puccinia Sorghi* was the most susceptible rust since it was successfully attacked by all of the isolations. *Puccinia Antirrhini* and *Uromyces Polygoni* were somewhat less susceptible, being attacked by only nine of the eleven strains, while *Frommea obtusa* and *Uromyces appendiculatus* were attacked by eight of the eleven isolations. Table 1 also shows that *Coleosporium Solidaginis*, *Kuehneola Uredinis*, and *Puccinia Clematidis*, all proved relatively non-susceptible to attack, and *Puccinia poculiformis* (*2*) was non-susceptible to all of the isolations.

If the average percentage of infection is considered an index of rust susceptibility, by comparing the figures shown in the last column of Table 1, it will be seen that *Puccinia Anemones-virginianae*, *Uromyces Polygoni*, and *Puccinia Sorghi* were the most susceptible, *Coleosporium Solidaginis* relatively non-susceptible, and *Puccinia poculiformis* (*2*) was entirely non-susceptible to attack. The average percentage of infection figures probably present a truer picture of relative susceptibility, than do the ratios indicating merely positive and negative results, as the former take into account not only the number of trials but also the actual number of rusted leaves inoculated.

Table 1 shows that the nineteen rusts varied in their susceptibility to any single isolation. For example, it will be observed that *Puccinia Anemones-virginianae*, *Puccinia Clematidis*, and *Uromyces Polygoni* were relatively the most susceptible, *Frommea obtusa* and *Puccinia poculiformis* (*2*) were less susceptible, and that *Coleosporium Solidaginis*, *Kuehneola Uredinis*, and *Puccinia Circaeae* were non-susceptible to the attacks of isolation No. 2. In the case of isolation No. 8, by the same sort of comparison it will be noted that *Puccinia Menthae* and *Puccinia Malvacearum* were most susceptible to the attacks of this isolation, while *Coleosporium Solida-*

ginis, *Kuehneola Uredinis*, and *Puccinia Clematidis* were non-susceptible. Comparing these results it will be seen that the rust species which appear to be most susceptible to isolation No. 2, are not necessarily the same species that seem to be most susceptible to isolation No. 8. The same is true of other examples.

Interpreting the specialization that is shown from the standpoint of the virulence of the *Darluca* isolations, it will be noted that some isolations seemed to be more virulent that others on the nineteen rusts. As shown in Table 1, isolation No. 5 was the most virulent, attacking successfully thirteen of seventeen rusts inoculated. Isolation No. 8 was somewhat less virulent attacking but twelve of seventeen rusts inoculated. Isolation No. 7 attacked only six out of fifteen, and isolation No. 3–B attacked six out of seventeen rusts, the latter two strains appearing to be the least virulent of the eleven.

If the relative virulence of the different isolations are determined from the average percentage of infection figures in the last row of Table 1, it will be noted that isolation No. 5 can still be regarded as being the most virulent on the nineteen rusts. Isolations No. 12–2 and 2 were somewhat less virulent while isolations No. 3–B and 4 proved to be the least virulent of the eleven.

It has been already pointed out that *Puccinia Anemones-virginianae*, *Puccinia Clematidis*, and *Uromyces Polygoni* may be considered as being the most susceptible of the nineteen rusts to isolation No. 2. It is also possible to consider that isolation No. 2 was more virulent on these three rusts, less virulent on *Frommea obtusa* and *Puccinia poculiformis* (*1*) while it was not able to attack some rusts at all. It is possible, therefore, to interpret the results either from the viewpoint of rust susceptibility or from the viewpoint of the virulence of the isolations.

Puccinia Sorghi was found to be a common host for all of the isolations. It has been said that *Puccinia Sorghi* was most susceptible to the attacks of isolations No. 3, 5, 6, and 7, less susceptible to isolations No. 2, 3–B, and 12–2, but we can also regard isolations No. 3, 5, 6, and 7 as being more virulent than isolations No. 2, 3–B, and 12–2 on this particular species of rust.

It is interesting to note that although isolations No. 3, and 3–B were made from the same species of rust (*Uromyces Silphii*) on the same phanerogamic host (*Juncus tenuis*), but from different localities, they proved widely different in their behavior on the nineteen rusts. Since such a difference in the virulence of isolations from the same rust species, but from widely different localities, has been shown, it would appear that there are probably unlimited possibilities for strain differentiation (biological specialization). The author (Keener, 1933) has already shown differences

in the growth of these two isolations on artificial laboratory media.

Infections were secured several times on *Puccinia Anemones-virginianae* on *Anemone virginiana*, on *Puccinia Circaeae* on *Circaea alpina* (Pl. 25, fig. 8), and on *Puccinia Malvacearum* on *Althaea rosea*. It is believed that this is the first reported occurrence of *D. filum* on these rust species. In addition, the author has collections of *D. filum* on the two micro-cyclic rusts, *Puccinia curtipes* on *Micranthes virginiensis*, and on *Puccinia Xanthii* on *Xanthium pennsylvanicum*.

The eleven isolations varied considerably as to their ability to attack the three micro-cyclic rust species. The isolations also showed marked variability in their relative virulence on these hosts. Isolations No. 1, 3, 4, 5, 8, and 11–1 successfully attacked both *Puccinia Anemones-virginianae* and *Puccinia Circaeae*. Isolation No. 8 also attacked *Puccinia Malvacearum*, being the only one of the eleven isolations capable of attacking all three micro-cyclic rusts used in this work. Isolation No. 2 attacked only *Puccinia Anemones-virginianae*. This strain was not inoculated onto *Puccinia Malvacearum* and lacked the ability to attack *Puccinia Circaeae*. Isolations No. 3–B and 12–2 infected *Puccinia Circaeae* but did not attack *Puccinia Anemones-virginianae*. Both isolations No. 6 and 7 lacked the ability to attack *Puccinia Anemones-virginianae* and *Puccinia Circaeae*. In addition, isolation No. 7 did not attack *Puccinia Malvacearum*. The last mentioned isolation was the only one of the eleven that lacked the ability to attack successfully at least one of the three micro-cyclic rusts. There is thus evidence that the isolations show considerable specialization on the micro-cyclic as well as the macro-cyclic rusts.

No correlations were found between the rust genera from which the isolations were made and the genera which they were found capable of attacking. That is, an isolation from a species of the rust genus *Puccinia* showed no particular tendency to attack only species of that one genus, but was also capable of attacking species of the other rust genera used. Isolations from macro-cyclic rusts attacked both micro- and macro-cyclic forms equally well. Since no isolations were made from micro-cyclic rusts, the reverse of this situation was not determined.

In the case of negative inoculations, the results may have been due to (1) the resistance of the rust, (2) a lack of virulence on the part of the isolation, (3) to a combination of both (1) and (2), or (4) to a combination of other factors. No doubt many factors entered into the results of the inoculations. The age of the rust sorus appears to be important in determining the susceptibility of a rust. In the case of macro-cyclic species it was noted that both the youngest and the oldest uredinia were free from infections, while those sori which appeared to be in a mid-developmental stage were heavily infested. It appears that the latter sori are the most

susceptible to attack. This condition, although much more difficult to determine, seemed to prevail in field collections of *D. filum* on such rusts. For example, on *Puccinia obscura*, a rust which is commonly heavily infested with the parasite, the oldest, rusted leaves never showed fresh *Darluca* infections. The parasite, when present on leaves in such a condition, has probably invaded the rust before the leaves have died off. In the greenhouse, rusts on dead leaves of both corn and timothy could not be infected when sprayed with conidial suspensions from isolations No. 1 and 8. In all of the rust inoculations, the dried, older sori were never attacked by the parasite. This is probably due primarily to the condition of the rust itself, and not to the lack of virulence on the part of the isolation.

Another possible limiting factor to infection, is the type of sorus produced by certain species of rusts. *Puccinia poculiformis* (*2*) on *Poa compressa*, produces a more or less compact, cushion-shaped sorus. As has already been pointed out this rust was not attacked by any of the isolations. It is possible that this type of sorus is so constructed as to preclude any possibility of invasion. The caeoma type sorus, as produced by *Coleosporium Campanulae* and *Coleosporium Solidaginis* appears to be comparatively resistant to parasitic attack at all stages of development. Although infections of this sorus type were secured on *Coleosporium Solidaginis* in greenhouse inoculations with isolations No. 3 and 6, and although field collections of the parasite on both *Coleosporium delicatulum* on *Euthamia tenuifolia* and on *Coleosporium Solidaginis* on *Solidago* sp., were made, the numerous negative trials on the latter rust species would seem to indicate that this type of sorus is comparatively resistant. *Kuehneola Uredinis* also proved somewhat resistant to invasion by *D. filum*. Here again, it appears that the type of sorus is the factor governing the susceptibility to invasion. While it is the writer's opinion that the type of sorus in these rust species, is to a large extent responsible for the results noted, there is little actual proof of this. It may well be that many other factors are involved.

The method of inoculation may also be a factor in determining rust susceptibility. It seems possible that inoculations on such rust species as *Puccinia poculiformis* (*2*) on which ordinary methods failed to give positive results, might be made successful by the use of the hypodermic syringe method. Time did not permit the carrying out of this method on this particular species of rust, but if the type of sorus is such that it serves as a protection against infections from outside sources, and if the parasite can subsist on the rust hyphae as well as on the rust spores, then it might be possible to infect such a rust by the introduction of *Darluca* conidia into the host plant directly. Under any conditions, the success of the hypoder-

mic syringe method no doubt depends to a large extent on the type and texture of the phanerogamic host. For instance, an inoculation into a hard, woody plant would no doubt result only in damage to the needle. The author suggests that in future work on biological specialization among the parasitic fungi, this method of inoculation should be investigated further.

Fluctuations in temperature had some effect on the amount of infection secured. However, at no time throughout the entire course of the inoculation work, did any strain giving positive results on a particular species of rust at one temperature, fail to give the same result on the same rust species, at another temperature. Dates of inoculations were recorded, and in general it may be said that the best and most uniform infections were secured during periods of comparatively low greenhouse temperatures.

An indirect factor governing the susceptibility of certain rusts may be the general condition of the phanerogamic host as expressed by the condition of the rust. Not only was the completion of successful inoculations more difficult, but also isolations of the parasite from field materials were harder to obtain, when the phanerogamic hosts were in a semi-wilted condition. The condition of the host plant in such a situation no doubt affects the viability of both the rust and the *Darluca*.

The pycnidia of the parasite are very often embedded in the spore mass of the rust sorus and are consequently macroscopically invisible (Pl. 25, fig. 8). Such a condition was particularly noticeable in greenhouse cultures of *D. filum* on *Puccinia Anemones-virginianae*, *Puccinia Circaeae*, and *Puccinia Malvacearum* of the micro-cyclic species, and on *Puccinia poculiformis* (*1*), *Uromyces caryophyllinus*, and *Uromyces verruculosus* of the macro-cyclic rusts. In order to avoid erroneously reporting a negative result in such cases, loose spores were scraped from the rust sori before examining the material under the binoculars. In this manner the pycnidia were made at least partially visible. The occurrence of embedded pycnidia may possibly explain the lack of reports of *D. filum* on certain rust hosts.

Biological Specialization. Arthur (1929) has stated "Apparently some species of rusts are more susceptible to parasitic attack than others. *Uromyces Junci* and other species on *Juncus* are especially invaded and often to such an extent that the formation of teliospores is much restricted, and the same is true of some species of *Puccinia* on *Carex*." Whether or not the author had biological specialization in mind when this statement was written, is questionable. However, the results of inoculations herein reported, with various isolations of the rust parasite, *Darluca filum*, show that in reality some rusts are more susceptible than others.

The author believes that the results of his inoculations show that *D. filum* consists quite definitely of many different strains. It seems evident

that since the eleven isolations all proved distinct in their choice of rust hosts, so far as this work is concerned, we can discern eleven strains of the parasite.

The degree of specialization is not as great as in the case of the natural *Darluca* hosts—the rust fungi. Many species of rusts show a comparatively limited choice of their phanerogamic hosts. Such was not the case with the isolations of the parasite. While the eleven isolations did prove more or less dissimilar when compared with each other, any particular strain showed a comparatively wide range of potential rust hosts.

Biological specialization is of widespread occurrence throughout both animal and plant kingdoms and it is well-known among many of the fungi. The rusts are recognized as one of the most highly specialized groups of parasitic fungi and there is a high degree of differentiation within their genera and species. Up to this time, the rusts have never been grown on synthetic laboratory culture media. In spite of the apparent constant association of *D. filum* with rusts, it seems quite evident that this parasite is not as highly developed parasitically as are the rusts themselves. The culturing in the laboratory of isolations of *D. filum*, and the tendency among them to infect more than a single rust host, seems to warrant such an assumption.

It has been previously pointed out that all of the isolations attacked *Puccinia Sorghi*. Perhaps after many more isolations have been made, a strain that will not invade this rust will eventually be found. It is also probable that in view of the inoculation results with isolations No. 3 and 3–B, that after further isolations have been completed from the same rust in widely-separated localities, many intergrading forms will be found to exist. If such is the case, then strain differentiations will become far more difficult. The author is of the opinion that further strain differences may be sought from two sources. Additional strains may be expected on different species of rusts, and also on any single rust species in widely separated localities.

With the exception of the production of a stroma by isolations No. 11–1, 11–2, and 12–2 both in the field and in culture, no appreciable morphological differences between the isolations, could be detected. It seems highly possible that *D. filum* is the only valid species of the genus *Darluca* and is composed of many strains differing from each other in various degrees, but not sufficiently divergent to be classed as biological forms.

The author is greatly indebted to Dr. H. W. Thurston, Jr., of the Department of Botany, The Pennsylvania State College, for his helpful advice in the carrying out of the experimental work and in the preparation of this manuscript; to Dr. L. O. Overholts and J. W. Sinden, also of the same department for their criticisms in the preparation of the manuscript; to

Dr. C. R. Orton of the University of West Virginia, Morgantown, for the collection of the material from which isolation No. 3–B was made; and to W. L. White, a graduate student in the Department of Botany, The Pennsylvania State College, for some of the rust determinations mentioned herein and the collection of the material from which isolation No. 2 was made.

SUMMARY

1. This paper reports the results of greenhouse cultures with nine conidial isolations of *Darluca filum*. Inoculations with two isolations (one from conidia and one from ascospores) of a fungus found on *Puccinia obscura* on *Juncoides campestre* and on *Puccinia Peckii* on *Carex normalis*, in Pennsylvania, are also recorded. (See footnote, p. 477.) The latter fungus was found to be producing pycnidia and conidia of the *D. filum* type, and in addition, perithecia, asci, and ascospores, resembling those of *Eudarluca australis* Speg.

2. A total of 175 greenhouse inoculations onto 16 macro-cyclic and 3 micro-cyclic rusts were made with eleven of the thirteen isolations. Of these 101 proved to be positive while 74 gave negative results. Of the 175 inoculations, 149 were made on the 16 macro-cyclic rusts, of which 85 were positive and 64 negative. Of 26 inoculations on the 3 micro-cyclic rusts, 16 were positive and 10 gave negative results.

3. The specialization shown is interpreted in two ways: first, from the point of view of the relative susceptibility of the rusts, and second, from the point of view of the relative virulence of the isolations.

4. Two methods of measuring relative susceptibility and relative virulence are discussed.

5. *Puccinia Sorghi* was the only rust attacked by all of the isolations and *Puccinia poculiformis* (*2*) was the only rust not attacked by any of them. The other rusts showed degrees of variation between these two extremes.

6. It is the author's opinion that the results of the greenhouse inoculations give evidence of the existence of eleven distinct strains of *D. filum*.

7. The degree of specialization is probably not as great as in the case of the natural *Darluca* hosts—the rust fungi.

8. Infections were secured several times on the three micro-cyclic rusts, and it is believed that this is the first adequate account of attack of these rusts by *D. filum*.

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Explanation of plate 25

Photomicrographs of free-hand sections of *Darluca filum*. Magnification (with exception of Fig. 5) ×214.

Fig. 1. Cross-section through innate pycnidia on *Puccinia Asparagi*.

Fig. 2. Superficial pycnidia on *Puccinia Sorghi*. Section of material from a positive inoculation.

Fig. 3. Cross-section through an erumpent pycnidium on *Uromyces Silphii* on *Juncus tenuis*.

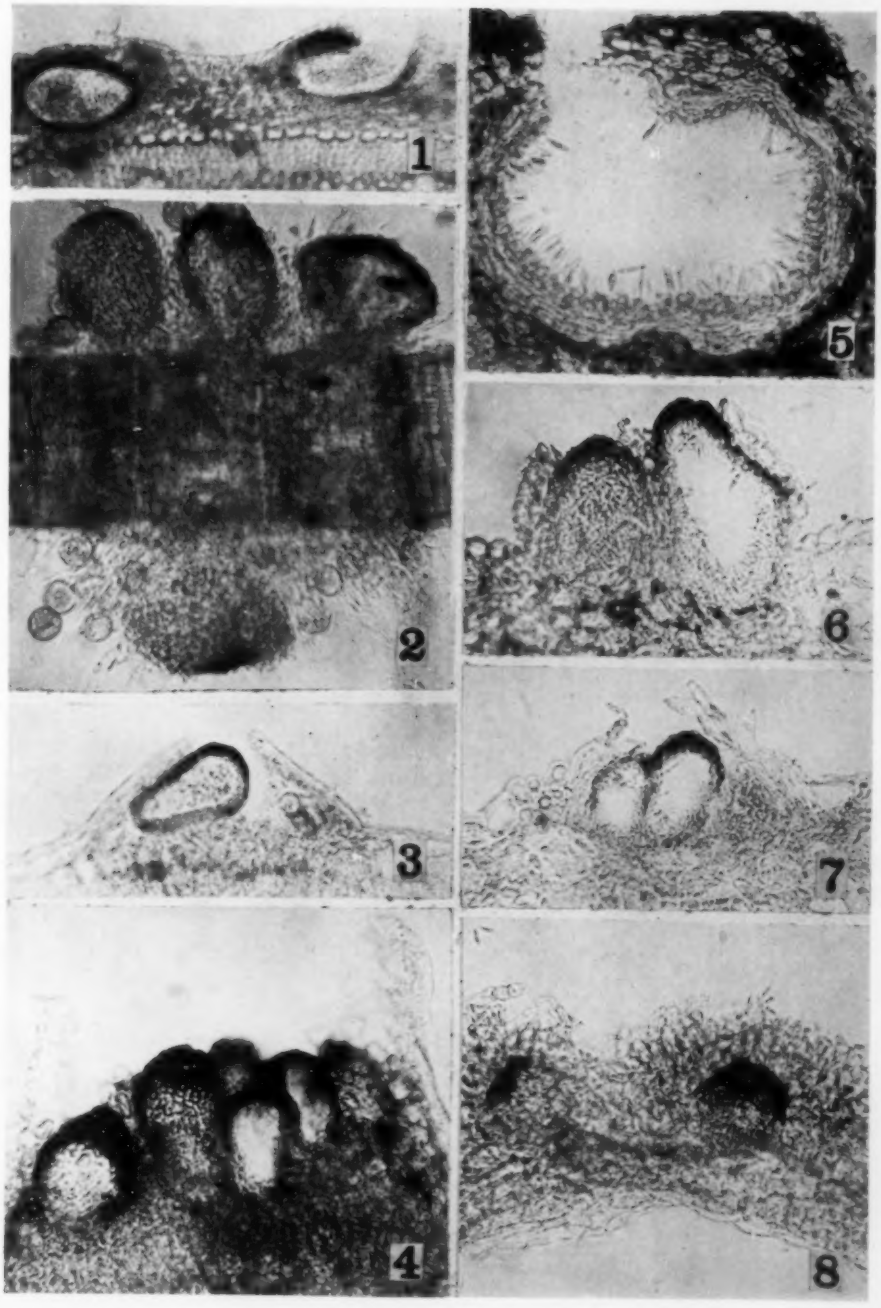
Fig. 4. Superficial pycnidia, showing fusion at the bases on *Uromyces Silphii* on *Juncus tenuis*.

Fig. 5. Cross-section through a pycnidium showing the production of conidia from the pycnidial wall cells. Material on *Puccinia obscura* on *Juncoides campestre;* ×445.

Fig. 6. Cross-section through pycnidia on *Puccinia epiphylla* on *Poa pratensis*. Northern collection (Keener, No. 112432-D).

Fig. 7. Cross-section through pycnidia on *Puccinia tubulosa* on *Paspalum Humboldtianum*. Collection from Venezuela, South America (Chardon, Toro, and Alamo, No. 345).

Fig. 8. Cross-section showing pycnidia embedded in spore mass of *Puccinia Circaeae* on *Circaea alpina*. Material from a positive inoculation.



KEENER: DARLUCA FILUM

UNIV. OF MICH.

A study of pollen-tube behavior in Lilium regale Wil.

ESTELLA HUMPHREY

(WITH TWO TEXT-FIGURES)

Lilium regale Wil. was first introduced into this country from Western China by E. H. Wilson of the Arnold Arboretum. It is a perennial which can be propagated by crown-branching, by rhizomes, or by seeds. Seeds ripen normally in the climate of New England (Wilson, 1925)—a statement that can be made for no other species of its class; and a filial generation will mature within two years.

Although the flowers of all lilies provide excellent material for studies on pollen-tube growth, those of *Lilium regale* are particularly favorable to such work, owing to the great size of the pistil and the prolific flowering habit. The subulate, often slightly curved, style expands into a capitate three-lobed stigma, the surface of which is covered with large papillate cells. The center of the style is characterized by an open three-angled canal extending throughout its entire length. After germination, the pollen tubes push between the cells of the stigma to the stylar canal, down the inner surface of which they proceed unhindered by obstructing tissue. The total length of the style to the uppermost ovule may reach 100 mm. As many as 27 flowers have been noted on a single stem under cultivation, although plants growing in the wild seldom produce more than one-fourth this number.

The biology of reproduction in this species has been studied only by Stout (1922) at the New York Botanical Garden. He found that the plants were preponderantly self-incompatible. Of the ten plants tested, nine were self-incompatible, while one was self-compatible. Cross pollinations sometimes succeeded and sometimes failed.

The plants used in the present study were raised from bulbs obtained from a local seed house. These bulbs appear to have been derived from seed borne on plants chosen for their self-incompatibility.

Preliminary test pollinations on flowers growing in the open showed varying results due to the changes in temperature. Pollen-tube growth was slower under cool cloudy conditions than on warm sunny days, and slower during a cool night than during the day. Consequently the studies were carried on in a constant temperature chamber.

Care was necessarily taken in the emasculation process, not to tear or to spread the young undeveloped flower parts. Careless handling resulted in an apparent retardation of growth on the part of both the pistil and the pollen tubes. Emasculation made too far in advance of the dehiscence of the anthers gave the same retarding effects. For this reason it was neces-

sary to emasculate the flowers just prior to the dehiscence of the anthers. The question arises as to the actual cause of this retardation of the development of the pistil. It seems probable that it is not caused by the disturbance to the flower as a whole, but rather that, through the removal of the anthers, some part is taken away which is important for normal development of the pistil.

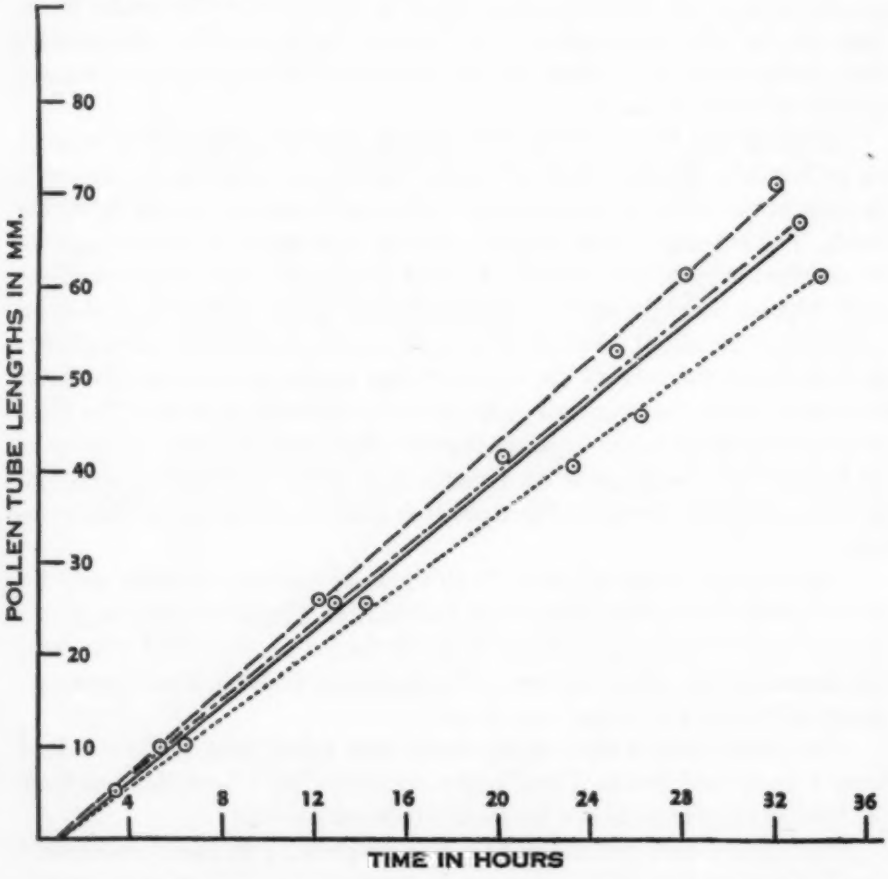


Fig. 1. Pollen-tube growth at 25°C. in cross-pollinations of *L. regale*. The solid line indicates the average growth of the three crosses.

As a rule, ten flowers of a single clon were picked, pollinated, and placed in a chamber where the humidity was uniform and the temperature was held continuously at 25°C. This manipulation was done at 9:00 A.M., since at this time the pistils were receptive to fertilization. The pollen was applied with camel's hair brushes to insure an even distribution on the stigma.

Pollen-tube growth in the pistils was studied every 6–8 hours over a period of 48 hours, or until fertilization occurred. A method of direct dissection and staining was employed. To facilitate handling in dissection, the styles—usually 80 mm. in length—were cut into 10 mm. sections. Each piece was then split longitudinally, spread flat on a slide, and stained with a few drops of aceto-carmine (saturated solution in 45% acetic acid. See Chandler, 1931). A second slide was pressed down upon the section, and the preparation was complete. When examined under the low power of a microscope, the extent of pollen-tube growth was readily determined.

Individual plants, or possibly clons, of *Lilium regale* differed in the rate of pollen-tube growth when selfed. Most of the plants were self-fertile, setting full capsules. Plant No. 5 selfed, however, showed a tendency toward self-sterility both in the pollen-tube growth and in the number of seeds set (East and Park, 1918). Figure 2 represents the growth curve of pollen tubes in this plant and also that of a selfed self-fertile plant. The latter is the only case found where there appeared to be a tendency for accelerated pollen-tube growth. Controlled selfings on the self-sterile plant produced seed capsules one fourth to one third normal size.

Cross pollinations gave generally similar results, as is seen in text-figure 1. Length plotted against time gives a straight line in which $x = \frac{1}{2}y$; or, in simpler terms, the tubes grew 2 mm. an hour. Only slight variations occur among individual plants. In figure 2, the solid line shows the average of the three broken lines in the figure. The closeness of the fit to a straight line in each case is readily apparent. In the case of delayed pollination (3:00 P.M. instead of 9:00 A.M.), the pollen tubes grew somewhat more slowly during the first 8 hours and then continued at a more rapid and normal rate until they entered the ovary.

The normal time of fertilization in selfed plants of *L. regale* is 36–40 hours after pollination. Should the growth of the pollen tubes be slowed down for any reason so that they do not reach the ovary in the time specified, the flower wilts, and fertilization fails. It follows that some pollinations may succeed and some fail on any given plant. As indicated by the curves in text-figure 2, the pollen-tube growth in the self fertile plants progressed at a constant rate. In the self-sterile plant, however, pollen-tube growth was much retarded. This is clearly indicated by the curve. After 34 hours the pollen tubes had progressed only 30–34 mm., or less than half the length of the style. At this rate, the tubes could never reach the ovary before the flower had wilted.

East (1934a, b) has shown that there are two major types of reaction affecting pollen-tube growth in the self-sterile plants of *Nicotiana* which he studied. The first is a simple nutritive reaction which produces a constant

growth-rate. The second is a reaction resembling that found in certain immunological processes. In this type a definite retardation occurs in incompatible matings due to mutual reactions between substances produced by the stigma and substances produced by the pollen tube. The acceleration which appears when compatible matings are made is apparently the reverse of the same reaction. *Lilium regale* shows a similar behavior. In addition, it is shown here that cross-pollinations as well as self-pollinations

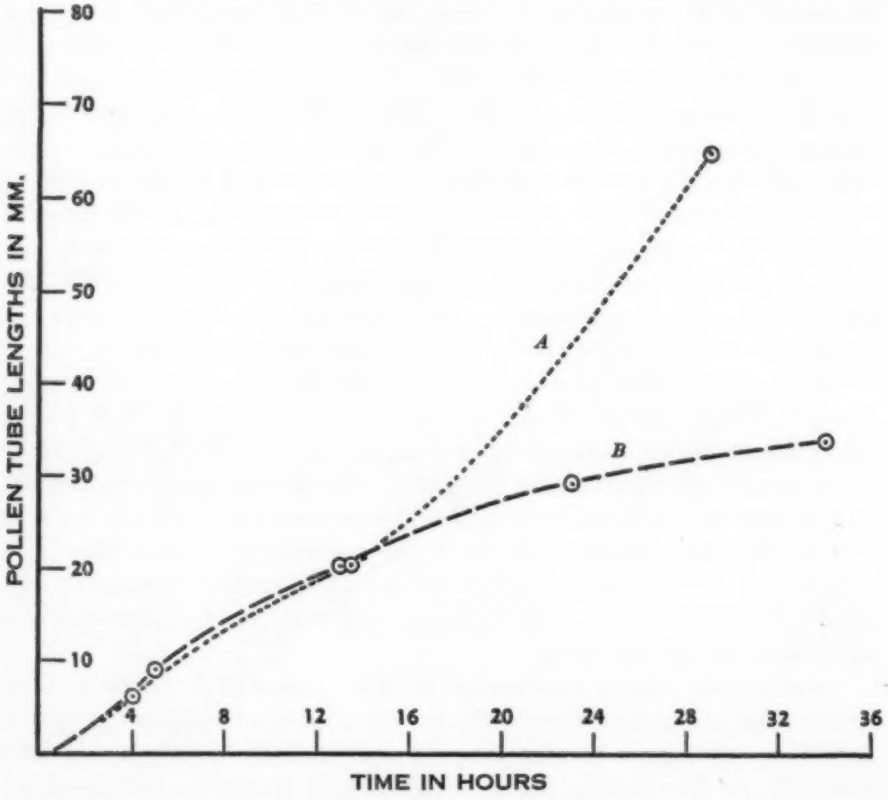


Fig. 2. Pollen-tube growth at 25°C. in two selfed plants of *L. regale*. A is self-sterile.

may exhibit the simple nutritive reaction which leads to constant growth of the pollen tubes. It is an interesting situation rather different from that ordinarily found in growth studies where there is an accumulation of adverse factors which gradually bring growth to an end. Of course it should be noted that the earliest portions of the straight-line curves must, in reality, show acceleration; but growth is constant from a period of about four hours after pollination until fertilization.

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Identification, by leaf structure, of the species of Abies cultivated in the United States

EDMUND H. FULLING

(WITH PLATES 26–32)

INTRODUCTION

The work reported in this paper was undertaken with a fourfold purpose:

1. To determine whether or not anatomical specificity exists, to any degree whatsoever, within the structure of the leaves of various kinds of fir.

2. If at least some such specificity be indicated to determine to what extent, if any, structural variation might preclude taxonomic use of foliar anatomy among these plants.

3. If sufficient specificity without invalidating variability be found, to prepare a key to the species of fir cultivated in the United States, the key to be based, primarily, upon leaf anatomy and supplemented only where unavoidable by external morphological characters of the leaves.

4. To prepare, in any event, a series of photomicrographs of cross sections of as many specific kinds of fir leaves as can be authentically identified representing the species cultivated in this country.

Concerning the first of these objectives, an examination of the literature upon the subject as well as the original work presented in this paper furnish an unequivocal affirmative answer. Concerning the second, differences of opinion have been expressed by previous workers and within the present paper is an evaluation of their findings in the light of the work herein reported. The third and fourth objectives constitute the principal part of this paper and merit no further comment here.

GENERAL DISCUSSION OF THE ANATOMY OF FIR LEAVES

The tissues of fir leaves, members of the genus *Abies*, may conveniently be considered under three different categories.

First, dermal tissues bound the leaf and in all cases consist of at least the epidermis, a single peripheral layer of cells, continuous except for stomatal openings. Externally, this layer is overlaid by a cuticular secretion which contributes to the general xeromorphic nature of the leaves by virtue of its universal presence, relative thickness and surprising toughness; the last-mentioned quality is especially noticeable in the difficulties inherent in paraffin sectioning of the mature organs. The stomatal apertures, according to the species, occur either only on the lower or on both surfaces

of the leaves. In either case, they occur in closely set parallel rows which on the lower surfaces generally appear as two whitish bands, one on each side of the midrib. In some, but not all, species there is next to the epidermis and constituting part of the dermal tissues, another layer or two of cells known as the hypoderm. The cell walls of this layer are generally thickened, in some species very conspicuously so, and through these walls radiating canals may usually be observed. When present and according to the species this layer is either continuous all around the leaf except directly beneath the stomata or it is more or less discontinuous because of interruptions by protrusions of mesophyll cells. When the layer is discontinuous the cells that do occur usually lie along the lateral margins of the leaf and in the center along both sides; also frequently elsewhere just within the epidermis. Regardless of the degree of continuity of this layer, it is either single-celled in thickness or two or three cells thick; the greater thickness, when present, is particularly well developed along the lateral margins and in the center along both sides. Physiologically, the hypoderm is the sclerenchymatous layer, providing partial protection against injury and extreme dessication. The epidermis shares in these functions.

Secondly, within the hypoderm is located the bulk of the leaf, the mesophyll tissue. Its constituent cells are relatively large and thin-walled as compared with those of the dermal tissues and are abundantly supplied with chloroplasts, for in these cells lies the power and function of photosynthesis. Physiologically, they constitute the chlorenchyma. This mesophyll chlorenchyma generally exhibits the two categories of palisade and spongy tissues; along the upper surfaces of the leaves and extending to the lateral margins the mesophyll cells are elongated and in vertical alignment for one or two rows; elsewhere, they are more rounded and irregularly disposed. The latter, constituting the spongy mesophyll, enclose many regularly arranged intercellular spaces which in cross sections appear as masses of torn tissue. In longitudinal sections, however, the spaces clearly alternate with strands of mesophyll. Within the mesophyll and to each side of the center is a resin canal; two canals per leaf are strikingly constant, more or fewer being anomalous though one species, *A. firma*, frequently exhibits four. The canals vary in diameter and location, according to the species, lying either against the dermal tissues, when they are known as marginal, or more or less within the chlorenchyma, being then designated as median.

Thirdly, through the center of the leaf and surrounded by the chlorenchyma extend the vascular and associated tissues which constitute the vein. They are separated from the mesophyll proper by a more or less distinct circular layer of cells, the endodermis, whose function in plants has long been a subject of much discussion. Within the endodermis, but not

occupying the entire space, are two strands of vascular tissue, more or less separate, according to the species, and entirely coalesced into one only in *Abies nobilis; Abies magnifica* very closely approaches the same condition. Each such strand consists of xylem cells on the upper half and phloem on the lower. Surrounding them, merging with them and filling the remainder of the space within the endodermis are the larger irregularly shaped cells of the pericyclic region. Within this region there occur, in some species, more or less distinct and sometimes very abundant and conspicuous thick-walled cells. Only in *A. firma* do such cells occasionally occur also in the chlorenchyma, at least sufficiently frequent to be of diagnostic value.

In brief, the contrasting features which appear sufficiently marked within the anatomical composition of fir leaves to be of taxonomic value as determined in this work and upon which the proposed key is based are:

1. Presence or absence of stomata on all surfaces of the leaves.
2. Presence or absence of hypodermal cells.
3. Continuous or discontinuous nature of hypoderm.
4. Moderate or excessive thickness of hypodermal cell walls.
5. One, two or more layers of cells in hypoderm.
6. Marginal, sub-marginal or median position of resin canals.
7. Size of resin canals.
8. Fused, slightly separated or distinctly separated nature of the two vascular strands.
9. Presence or absence of thick-walled cells within the pericyclic region.
10. Moderate or striking occurrence of these cells.
11. Presence or absence of thick-walled cells in the chlorenchyma.
12. Number of lines of stomata per band on leaves.
13. Thickness of epidermal cell walls.
14. Contrasts in shape of cross sections.

REVIEW OF THE LITERATURE

Thomas (1865) appears to have been the first to attribute taxonomic importance to the anatomy of coniferous leaves. He published a general discussion of the tissues involved describing, in particular, the epidermis, hypoderm, parenchyma, vascular bundle and resin canals. In addition, he discussed the more particular anatomy to be found in the leaves of the Cupressineae, Abietineae, Araucarineae, Podocarpineae and Taxineae.

Bertrand (1871) went a step further and published, not only a short general as well as a specific discussion of leaf anatomy among the firs, but

formulated a key to eighteen species based wholly upon foliar morphology. Three years later the same author presented a larger treatment of the subject covering the Gnetales and Ginkgoales as well as some twenty-five genera of the Coniferales. In it appeared a revision of his earlier key to the firs. This first attempt to distinguish species of conifers by their leaf structures contained several errors and, as Viguié and Gaussen (1929) remark, it is more of historical interest than scientific importance.

McNab (1875–1877), in a series of papers, gave a revision of the genus *Abies* and discussed the foliar anatomy of several particular species.

Engelmann (1878) appears to have been the first to consider, in particular, the foliar anatomy of the American firs. He prepared a rather detailed study of them including an anatomical key.

Fedtschenko (1879), apparently having implicit faith in the taxonomic value of leaf anatomy, founded a new species, *A. Semenovii*, upon such criteria. Beissner (1898), however, criticized this work and Fedtschenko's species has since been disregarded.

Medwedew (1880) studied only *A. Nordmanniana*. Meyer (1883) was impressed by the taxonomic significance of the resin canals in the leaves. Masters (1889 and 1891) made further general and specific observations. Trabut (1889) studied four Mediterranean species and published very fine plates of their foliar anatomy. Some years later (1906 and 1928) he, like Fedtschenko, appears to have established a new species, *A. Marocana*, partly at least upon leaf structure.

After Engelmann, Lemmon (1889–1890) was the next American writer to discuss leaf anatomy, which he did in connection with a very excellent report upon all the conifers of California.

Daguillon (1890), in a series of articles, furnished considerable data upon the subject. The following year Van Tieghem (1891) did likewise and, in addition, formulated an anatomical key to twenty-five species.

Sargent (1892), in his classic "Silva," was the third important American contributor. Bastin and Trimble (1896) next took up the American side of the investigations and in a series of articles published data and pictures of fir-leaf anatomy. Hickel (1906 and 1908) made extensive studies of the genera in the Abietineae and formulated keys to the species, based partly upon leaf anatomy. Guinier and Maire (1908) made various allusions to the leaf anatomy of the Mediterranean firs. Lamb (1912–1914) did likewise in the case of the American species. The extensive bulletin by Zon (1914) upon the balsam fir naturally also contained anatomical data. Bode (1914) gave some consideration to an unimportant species, *A. Nebrodensis*. Sharp (1915), who published anatomical studies of all the native genera, appears to have been the fifth to give serious attention to the American conifers.

The paper by Durrell (1916) is valuable because of its drawings of every species. Sudworth (1916) continued these considerations with his dendrological bulletin. Pujuila (1921) studied some varieties of the Spanish fir. Mattfeld (1925) published a valuable paper with anatomical, distributional and other considerations of the Mediterranean firs. In Japan two studies upon the subject in hand have been made, those of Ohki (1925) and of Hayata and Satake (1929). The establishment of the two latest species to be added to the genus *Abies* was based partly upon leaf anatomy by Gaussen (1928) and by Flous and Gaussen (1932).

Finally, the most extensive morphological study of the firs is the revision of the genus by Viguié and Gaussen (1928 and 1929). In this monographic work 52 species and 12 varieties of fir are morphologically described with respect to leaves, branches, buds, flowers and cones. For some reason, a bibliography very unfortunately does not accompany this paper though an extensive review of literature is included.

Certain histological regions within the leaves of firs have received special attention in attempts, not only to describe them anatomically but, more important, to discover their functions and phylogenetic importance. Soar (1922) published a worthy contribution in this respect upon the endodermis in the leaves of the Abietineae. Among her observations the one most pertinent to the problem in hand probably is that hypodermal tissues in the leaves of *Picea* and *Abies* are most strongly developed near the bases where there is incomplete development of the endodermal sheath. This fact emphasizes the necessity, for taxonomic purposes, of considering foliar cross sections from the middle of the leaf and not near the base.

Within the endodermis, as already indicated, is located the vascular tissue consisting of both xylem and phloem cells surrounded by the larger and looser cells of the pericyclic region. In gymnospermous leaves varying amounts of this region are occupied by short parenchymatous tracheids possessing bordered pits. Such cells constitute the so-called "transfusion tissue" which, according to Haberlandt, is poorly developed in *Abies* but greatly in *Pinus*. The interpretation, functionally and phylogenetically, of this transfusion tissue has engaged several investigators. Frank (1864) appears to have first observed it in *Taxus baccata* where he regarded it as arising from the bundle proper.

From that time until 1913 a number of contributions with conflicting ideas were published by Thomas, von Mohl, Bertrand, de Bary, Zimmerman, Scheit, Vetters, Daguillon, Van Tieghem, Lignier, Worsdell, Bernard, Chauveaud, Carter, and Takeda. In brief, their ideas represent two schools of thought, the one regarding transfusion tissue as centripetal xylem and a part of the vascular bundle itself, the other looking upon it as pericyclic

or parenchymatous in origin. Concerning the function of the tissue some have held it to be for storage, others as an auxiliary conducting system.

Chauveaud (1904), concerning himself with the double nature of vascular bundles in the leaves of firs and pines, decided, in the cases of *A. venusta* and *A. Pinsapo*, that the vascular strand is at first undivided and becomes divided during the course of development through secondary modifications. Hill and de Fraine (1908 and 1909), as well as Hickel (1911), studied, among other features, cotyledons of the firs. Gyorffy, in a number of articles, was interested in the occurrence and morphology of double needles. Stomata occupied the attention of Wilhelm (1883), Hildebrand (1860) and Mahlert (1885). F. Darwin (1887) was concerned about the relation between "bloom" and stomata. Florin (1932) discusses stomata in his recent paleobotanical studies.

The influence of environmental conditions upon the anatomy of fir leaves has not been overlooked. Hartmann (1892) and, to a more informative degree, Anderson (1897), were concerned with abnormal foliar anatomy resulting from pathogenic infection. Climatic influences upon foliar anatomy engaged the attention of Areschoug (1882) in a general way. Mer (1883) was concerned with similar influences of light and shade upon the leaves of Norway spruce. Noack (1888) was interested in the influence of climate upon cuticularization and Hessmer (1916) studied the differences between exposed and shaded leaves of evergreens. Taubert (1926) pursued similar investigations upon the leaves of *Abies* in one of the best contributions upon the subject. Liese (1929) and Mussiuk (1932) observed similar differences in the Scotch pine.

Dependability of anatomical features for taxonomic purposes has been implied if not directly defended in every work proposing keys. It is obvious that to those sharing this viewpoint structural constancy of foliar organs appears greater than any variability that may at the same time occur in them. Other observers, however, impressed more by exceptions to the rule regard foliar structure as unreliable for purposes of determination. Von Wettstein (1887), apparently writing of Austrian plants, said the coniferous species of his flora could be more accurately determined by foliar anatomy and that such examination presents the surest means of recognizing hybrid forms. Masters (1891) admitted that some anatomical features possess diagnostic value to a certain degree. Petunnikov (1900), however, impressed by the work of Duval-Jouve (1875) upon the grasses and by that of Bertrand (1874), Koehne (1893) and Fedtschenko (1898) upon *Abies*, denies any such value. Fritsch (1903) discusses this matter in a general sense and makes the following statement which expresses the viewpoint adopted by the present writer in undertaking the work in hand: "In

no case can one depend on anatomy alone in generic and specific distinction, but if we take it hand in hand with the external characters we shall very frequently find that the two supplement one another in a most agreeable manner." Hamilton (1916) wrote about the instability of leaf morphology in its relation to taxonomic botany. Maleev (1929) expresses other views.

Gauba (1927) writes of "Metakutisierung" of resin canals, probably meaning cuticularization of their walls and says that examination of 27 coniferous genera with over 100 species indicates that this feature possesses no systematic value.

Several other genera of plants have also been investigated with reference to their foliar anatomy. Among the angiosperms only the early and recent very extensive studies of Duval-Jouve (1875) and Prat (1932) upon the grasses can be mentioned. Every family of the gymnosperms appears to have received attention, and of the genera most closely related to *Abies* the following studies deserve recognition.

Pinus: McNab (1875), Purkyne (1875), Menge (1878), Engelmann (1880), Mahlert (1885), Coulter and Rose (1886), Van Tieghem (1891), Bastin and Trimble (1897), Masters (1904), Pardé (1912), Shaw (1914), Doi and Morikawa (1929), Hayata and Satake (1929), Grigorieva (1930), Harlow (1931), Fieschi and Gaussen (1932), Fieschi (1932), and Sutherland (1934). Among these, the works of Harlow and of Sutherland are most worthy of consideration because of their specific descriptions, anatomical keys and photomicrographs. The so-called pines of Australia, which include a number of southern hemisphere gymnosperms, none of which belong to the genus *Pinus*, are extensively treated by Baker and Smith (1910).

Picea: Brunet (1866), Bastin and Trimble (1897), Hayata and Satake (1929), Gaussen and Lacassagne (1930) and Marco (1931), *Tsuga:* McNab (1876), Bastin and Trimble (1897). *Pseudotsuga:* McNab (1876), Koch (1877), Flous and Gaussen (1932). *Taxodium:* Coulter (1889). *Cupressus:* Maxwell (1896), Camus (1914). *Torreya:* Hayata and Satake (1929). *Sciadopitys:* Hayata and Satake (1929). *Juniperus:* Hayata and Satake (1929).

In addition to all the above-mentioned more or less special contributions upon the subject in hand, one finds abundant taxonomic reference to foliar anatomy of firs in many general treatises. Among these are those of Carrière (1855 and 1867), Mayr (1890), Beissner (1891, 1899, 1909, 1930), Koehne (1894), Sargent (1898, 1905 and 1916), Elwes and Henry (1909), Pardé (1913), Clinton-Baker (1913), Wilson (1916), Coltman-Rogers (1920), Dallimore and Jackson (1923), Bailey (1923), Engler and Prantl

(1926), Rehder (1927), Fitzpatrick (1929) and Mattfeld (1928 and 1930).

Numerous general remarks, not especially taxonomic but otherwise informative, have come to the writer's attention in the following references: Goeppert (1841), DuHamel (1777), Zuccarini (1843), Schacht (1853), Hempel and Wilhelm (1889), Masters (1880 and 1891), Dammer (1900), de Bary (1884), Feustel (1921).

PROCEDURE

Sources and selection of material

To determine what species of fir are in cultivation in this country Rehder's list was originally accepted. In the recent edition of Bailey's manual (1933), which appeared during the course of this investigation, one more species, *A. religiosa*, is described which was not included in earlier editions of either work. Of the 38 species thus listed as being cultivated, some are not yet extensively grown. These, however, have been included in the present study because of the prospects of their increased use in horticulture. Varieties have been omitted principally because of their relative unimportance and the added complications their inclusion might have caused.

In the belief that fresh living leaves would offer more natural objects for study, efforts were made to secure, so far as possible, such material. Local pineta presented the most immediate sources in this respect. From the following collections, accordingly, living material of almost every species reported to be in cultivation was secured:

Arnold Arboretum, Jamaica Plain, Mass.
Pinetum of the New York Botanical Garden.
Pinetum of Childs Frick, Roslyn, N.Y.
Pinetum of T. A. Havemeyer, Brookville, N.Y.
Pinetum of R. H. Montgomery, Cos-Cob, Conn.
Pinetum of A. G. Hodenpyle, Locust Valley, N.Y.
Pinetum of W. R. Coe, Oyster Bay, N.Y.
Pinetum of George Brett, Fairfield, Conn.

In addition, requests for material were sent to forest supervisors and other persons in similar positions scattered throughout the western states. By their kind assistance fresh specimens of our native species, packed in damp moss or other suitable moist substance, were thus secured. The letters sent to these various persons, in addition to stating the nature and purpose of the request, were accompanied by mimeographed sheets to be filled in by the collector for the purpose of furnishing information concerning the geographical and altitudinal locations of the trees sampled and

whether each twig sent was secured from the lower sunny, lower shaded, upper sunny, or upper shaded side of the tree. These four classes of twigs from each tree were especially requested because the writer wished to determine, so far as was practically possible, if there might be sufficient anatomical variation within these parts of the tree to discredit any otherwise apparently valid distinguishing features. The cooperation on the part of the persons solicited was especially gratifying, furnishing the following material:

Species	*Elevation*	*Location*
arizonica	9000′	Beaver Creek Reservation, Rio Grande National Forest, Arizona.
amabilis		Vancouver Is., B.C., Canada.
balsamea		Ottawa, Canada.
		Moore Factory, Canada.
Fraseri		North Carolina.
		West Virginia.
grandis		Vancouver Is., B.C., Canada.
		University of California campus.
		Wenatchee Mts., Washington.
concolor	8500′	Alamo Camp, Rio Grande National Forest, Arizona.
		Cloudcroft, New Mexico.
	8000′	Manti National Forest, Utah.
	9000′	Manti National Forest, Utah.
	7000′	Manti National Forest, Utah.
	6600′	Sequoia National Forest, Cal.
		Heber, Utah.
		Albuquerque, New Mexico.
lasiocarpa	7500′	Gallitin National Forest, Mont.
	8000′	Sawtooth National Forest, Idaho.
	9200′	Medicine Bow National Forest, Wy.
	8500′	Manti National Forest, Utah.
	7200′	Targhee National Forest, Idaho.
		Heber, Utah.
		Vancouver Is., Canada.
magnifica	7500′	Sequoia National Forest, Cal.
	7600′	Sequoia National Forest, Cal.
nobilis		Wenatchee Mts., Washington.
venusta		University of California campus.

Lastly, the writer personally secured specimens of *A. balsamea* from Livingston Manor in the Catskill Mts. of New York and from the Douglas Lake region of northern Michigan; also *A. Fraseri* from the northern limits of its range in West Virginia.

Determination of species

Inasmuch as the value of any conclusions derived in this work would be largely dependent upon the certainty of the identification of the specimens examined, great care was exercised in determining the species of material employed. By diligent consultation of standard taxonomic and dendrological works, coupled with the field work involved in collecting, the writer sufficiently familiarized himself with the kinds of fir in cultivation so that he finally felt certain of the material eventually selected for study. The principal references consulted for this purpose were those of Sargent (1898), Rehder (1927), Dallimore and Jackson (1923) and Beissner-Fitschen (1930). Every branch from which leaves had been examined was dried and mounted and compared with herbarium specimens kindly lent by the Arnold Arboretum, as well as with those in the herbarium of The New York Botanical Garden.

Technique

Celloidin Method

The following schedule of technique, adapted from Harlow with some modifications, was employed in this work:

1. Tie needles in bundles of 15 to 30 with thread a little to one side of their centers.
2. Cut off, with razor, each end of bundle leaving a fagot about $\frac{1}{4}$ to $\frac{1}{2}$ inch long.
3. Dehydrate fagot in 50% alcohol under reduced pressure of water pump until bubbles cease to rise from needles.
4. Provide at least two changes of absolute alcohol during next 48 hours.
5. Change to 50–50 mixture of absoute alcohol and ether for 12–24 hours.
6. Immerse in thin solution of celloidin dissolved in 50–50 mixture of absolute alcohol and ether, about consistency of glycerin, in small glass bottles provided with tight cork and metallic screw cap.
7. Leave bottles in paraffin oven for one week.
8. Remove from oven, allow to cool partly, open and permit celloidin to thicken slowly by evaporation of alcohol-ether. Assist by occasional stir-

ring to prevent formation of surface film as celloidin must be kept homogeneous during this process, which occupies a few hours. Thicken to a consistency obviously greater than originally, re-cork and cap and put in oven; or replace celloidin with thicker celloidin. This latter method is quicker though more troublesome because of the nature of celloidin.

9. Repeat last operation in a few days or a week until celloidin is so thick that a mass of it removed on an instrument will no longer run but congeal on exposure to the atmosphere.

10. Remove bundle with adhering celloidin by means of forceps into small amount of chloroform which solidifies the celloidin. Leave for 2 to 12 hours. Longer immersion does no harm; on the contrary, it insures more uniform solidification of the celloidin.

11. Cut on sliding microtome with oblique knife, through part of fagot corresponding to center of original needles. Lubricate blade and celloidin block with 70% alcohol for each section. Cut 24 to 30 microns thick. If sections roll on blade unroll them with brush just before completing stroke through block. Remove with brush into 70% alcohol.

Two methods of staining technique were employed. The first was:

12a. Add to 70% alcohol containing sections a few drops of 1% Bismarck brown in 70% alcohol; stain to desired intensity.

13a. Pour off Bismarck brown and wash in 70%, 95% and two washes of 100% alcohol, two to five minutes in each, half hour at least in last of absolute. To each washing of absolute add a few drops of chloroform to prevent softening and possibly dissolution of celloidin matrix. If, in spite of precautions, the matrix does soften causing sections to adhere together or loosen and thus render their subsequent individual handling difficult, the chloroform should be omitted and the celloidin allowed to dissolve in the alcohol, even with the assistance of a little ether. If so used, the ether must be removed by washings in absolute alcohol previous to the subsequent application of xylol. By this latter procedure the sections are at least rescued from a gummed mass of celloidin though their mounting without a matrix becomes more difficult.

14a. Pour off alcohol and give at least two washings of xylol, at least half an hour in last one.

15a. Mount in balsam.

For photomicrographic purposes the above as well as the following schedule, adopted from Harrar, were found satisfactory:

12b. Dilute 70% alcohol containing sections with about same amount of distilled water.

13b. Add a few drops of aqueous ferric ammonium sulfate, a mordant, and allow to remain about five minutes.

14b. Pour off, wash twice in distilled water, add some distilled water and a few drops of aqueous haematoxylin. Watch staining under microscope to desired intensity.

15b. Pour off, wash twice in distilled water, pour on 70% alcohol and add a few drops of Bismarck brown.

16. Same as in 13a to 15a.

It was found more satisfactory in some cases for photographic purposes to remove the celloidin by ether, preferably after staining, and then to select under a hand lens a few of the best sections for mounting. Most pictures were obtained, however, of sections in a celloidin matrix.

Pressure chamber and paraffin

Before the details of the above described celloidin technique were satisfactorily developed, a pressure chamber, as suggested by Lodewick, was devised. Supposedly, such an apparatus would secure more rapid penetration of the material by the celloidin. The method, however, was not satisfactory so far as it was attempted.

Though young immature coniferous needles are known to section well in paraffin, older ones, according to Chamberlain, do not lend themselves to such treatment. This was found to be true in attempts to employ paraffin in the butyl-alcohol technique. Rather than attempt modifications of this method, such as Hance suggests, this technique, too, was abandoned and all the work was performed as outlined above.

Herbarium material

In spite of efforts to secure fresh leaves a few species remained unrepresented in the writer's collections. Inasmuch as these, too, were reported to be in cultivation, though apparently not extensively so as yet, it became necessary to resort to herbarium material in order to include them. In so doing it was found that the quality of herbarium material for anatomical purposes varies considerably, probably depending upon drying methods employed in connection with such specimens. Internal structure was almost perfectly preserved in some cases; badly distorted in others. Unsatisfactory material was usually indicated by excessive shrinkage of the mesophyll along the midrib resulting in prominence of the latter. This was apparent by hand-lens inspection of leaves merely cut across. Those that appeared least distorted were run through the celloidin method with the addition of the following between items #2 and #3 of that schedule:

Boil fagots in water for 5 to 10 minutes, transferring them momentarily once or twice during the boiling into cold water to insure penetration.

RESULTS

Concerning anatomical variability

That anatomical variability might invalidate apparently acceptable diagnostic features in fir-leaf anatomy was well recognized before the work herein reported was undertaken. Previous investigators differed in their opinions upon this point. Some appear to have regarded variability as sufficient to disqualify attempts at classification by foliar anatomy; others apparently looked upon it only as exceptions to general rules. In choosing between these two viewpoints one might be inclined to be more impressed by those who found exceptions, for such results usually indicate more thorough investigation. It became necessary for the present writer, consequently, to arrive at some decision with regard to this controversial matter. To do so he hoped to be able to study material of each species from so many different locations as well as from different parts of the same trees that all possibilities of variation would come under his observation. It soon became apparent, however, that such ideal methods were beyond attainment. In compromise, he realized this objective in two native species only and then arbitrarily adopted a suggestion of Taubert.

The two native species which lent themselves to a study of variability were *A. concolor* and *A. lasiocarpa*. In addition to specimens gathered in cultivated collections others, as already noted, were secured from a number of locations within their natural ranges of distribution. Altitudinal and geographical influences, to some degree at least, were thus observable. Three- and four-year old needles from the lower sunny and shaded and the upper sunny and shaded portions of each tree were examined. In each of these groups three bundles of needles were prepared thus making 24 bundles per tree each containing at least 10 needles. From each such bundle at least 20 sections were cut. Over 4000 cross-sections of leaves were thus prepared from each tree considered. While it cannot be said that so many were always critically examined, the chances of discovering important variations were certainly greatly increased. In spite of this painstaking effort to detect structural deviations the anatomical features in these two species were so constant, at least concerning the characters necessary for identification, that in them variability was negligible. The positions of resin canals, the thickness of hypodermal cell walls, the degree of separation of vascular strands and various other details were observed to vary slightly, but no correlations with environment and positions on the tree could be made with justification.

These two species are among the most easily identified of the firs. Because of this the writer would scarcely have been justified in assuming that

Summary of anatomical characters in the leaves of cultivated species of Abies

SPECIES	STOMATA	HYPODERM	CANALS	BUNDLES	THICK-WALLED CELLS IN PERICYCLIC REGION	REMARKS
A. alba	On lower surface only	Discontinuous, double in places	Marginal	Separated	Few	
A. amabilis	On lower surface only	Continuous	Marginal	Separated	Absent	
A. arizonica	On both surfaces	Continuous	Median	Separated	Absent	Indistinguishable anatomically from A. lasiocarpa.
A. balsamea	On lower surface only	Discontinuous or absent	Median	Separated	Absent	Distinguishable from A. Fraseri only when hypodermal cells are absent.
A. Beissneriana	On lower surface only	Continuous, double in places	Marginal	Separated	Present	Lateral margins are bluntly pointed.
A. Borisii-regis	On lower surface only	Continuous, double in places	Median	Separated	Present	
A. Bornmülleriana	On lower surface only	Continuous	Sub-marginal	Separated	Present	
A. cephalonica	On lower surface only	Continuous, double in places	Marginal, small	Separated	Present	Pointed leaves tending to be radially arranged are distinctive.
A. chensiensis	On lower suface only	Continuous	Marginal	Separated	Present	Bluntly pointed lateral margins of cross sections are quite distinctive.
A. cilicica	On lower surface only	Continuous, double in places	Marginal	Separated	Present	
A. concolor	On both surfaces	Discontinuous	Marginal	Separated	Rare	
A. Delavayi	On lower surface only	Continuous	Marginal	Separated but close	Present	Leaves are markedly revolute.
A. Fargesii	On lower surface only	Discontinuous	Median to sub-marginal	Separated	Present	
A. Faxoniana	On lower surface only	Continuous	Median	Separated	Present	
A. firma	On lower surface only	Continuous, very thick-walled	Median	Separated	Present and in chlorenchyma	Only species with thick-walled cells in chlorenchyma.
A. Forrestii	On lower surface only	Discontinuous	Median	Separated	Present	Leaves are slightly revolute.
A. Fraseri	On lower surface only	Discontinuous	Median	Separated	Absent	Distinguishable anatomically from A. balsamea only when hypodermal cells are absent from latter.

A. grandis	On lower surface only	Absent or few cells present	Marginal	Separated	Rare	
A. holophylla	On lower surface only	Continuous, double in places, thick-walled	Median	Separated	Abundant	Long pointed needles on young plants are very distinctive.
A. homolepis	On lower surface only	Continuous	Median	Separated	Abundant	
A. koreana	On lower surface only	Absent, few cells may be present	Marginal-sub-marg.	Separated	Absent	
A. lasiocarpa	On both surfaces	Discontinuous	Median	Separated	Absent	
A. magnifica	On all surfaces	Discontinuous 2–4 cells thick in angles	Marginal	More or less fused	Absent	Only species with more or less four-sided leaves bearing stomata on all surfaces. Vascular strands more or less fused.
A. Mariesii	On lower surface only	Absent	Median-sub-marg.	Separated	Absent	
A. nephrolepis	On lower surface only	Discontinuous	Median	Separated	Present	
A. nobilis	On both surfaces	Discontinuous	Marginal	Fused	Absent	Only species with completely fused vascular strands. Marked groove along upper surfaces of leaves.
A. Nordmanniana	On lower surface only	Discontinuous	Marginal	Separated	Absent	
A. numidica	On lower surface only	Continuous, double in places	Median	Separated	Absent	Stomata sometimes on upper surface.
A. Pindrow	On lower surface only	Continuous	Marginal	Separated	Present	
A. Pinsapo	On both surfaces	Continuous or disc. Double in places	Marginal-Median	Separated	Absent	Very distinct species because of stomata on upper surfaces of leaves which radiate in all directions from twig.
A. recurvata	On lower surface only	Continuous, double in places	Marginal	Separated	Present	Very distinct when leaves are bent back along twig.
A. religiosa	On lower surface only	Continuous	Marginal	Separated	Present	
A. sachalinensis	On lower surface only	Absent	Median	Separated	Present	Canals large.
A. sibirica	On lower surface only	Absent	Median	Separated	Absent	Canals large.
A. spectabilis	On lower surface only	Continuous	Marginal	Separated	Present	Cross-sections sometimes bluntly pointed at lateral margins.
A. squamata	On lower surface only	Continuous	Median	Separated	Present	Leaves unusually thick and resin canals distinctly median.
A. sutchuenensis	On lower surface only	Continuous	Median	Separated	Present	Said to be distinguished by its yellow petioles.
A. Veitchii	On lower surface only	Absent	Median	Separated	Present	
A. venusta	On lower surface only	Continuous	Marginal	Separated	Absent	No groove along upper surfaces of leaves.

their anatomical constancy indicated equal freedom from variability among other species. It was impossible to investigate this matter, however. In order, then, to reconcile dissension among previous investigators Taubert's suggestion was accepted that to give value to leaf structure one must specify the part of a tree from which the leaves to be considered are secured. To fulfill this condition the writer arbitrarily based his work, so far as was possible, upon leaves secured from the lower part of a tree, preferably the shaded side, for on every plant there is one side that is at least not in direct sunlight. In the case of herbarium material such information is almost never stated, and for that reason herbarium material was used as little as possible.

It must be stated, however, that no anatomical feature can safely be determined by an examination of only one or even a few leaves. As many as is practically possible should be examined, for frequently it is only by an average of many observations that one may be able to assign a particular character to one or another category. This is especially true concerning continuity of the hypoderm and location of resin canals. In the case of *A. firma*, for example, the occurrence of thick-walled cells in the chlorenchyma is very distinctive, but they do not appear in every section. Sections examined must be from the middle part of the leaves for toward the ends the position of resin canals and abundance of hypoderm varies. Leaves three or four years old were always used.

Finally, the writer feels it necessary to state that he does not propose the key presented in this paper as a substitute for the longer established means of identification based upon cones, buds, twigs and leaves. He offers it only as a supplement to those methods, especially in cases where certain external characters cannot be observed. This is particularly true in spring and early summer before the winter buds form.

KEY TO THE CULTIVATED SPECIES OF ABIES BASED UPON STRUCTURE OF LEAVES FROM STERILE BRANCHES

A. Stomata nearly equally numerous on all surfaces.[1]
  B. Resin canals median.
    C. Leaves usually not over 2 cm. long, radially arranged on twig..... *A. Pinsapo*
    CC. Leaves usually over 2 cm. long, not radially arranged on twig..... *A. lasiocarpa*
      A. arizonica[1]

[1] The presence or absence of stomata on all surfaces of the leaves can be determined most accurately by macroscopic examination. Species under "AA" sometimes have a few stomata on the upper surface near the tip and occasionally near the center, the latter being observable in median cross-sections. They never approach the abundance, however, of those on the under surface as in species under "A."

BB. Resin canals marginal.
C. Vascular bundles appearing as one or nearly so.
D. Cross-sections rhomboidal in shape; vascular bundles sometimes slightly separated.....*A. magnifica*
DD. Cross-sections not rhomboidal in shape; groove along upper surface frequently very sharp; vascular bundles always appearing as one....*A. nobilis*
CC. Vascular bundles distinctly separated.
D. Leaves usually not over 2 cm. long, radially arranged on twig....*A. Pinsapo*
DD. Leaves usually over 2 cm. long, not radially arranged on twig..*A. concolor*
AA. Stomata abundant only on lower surface.[1]
B. Hypodermal layer absent; occasional individual cells, more or less thick-walled, directly beneath epidermis, sometimes in groups, but never sufficiently abundant to constitute what might be regarded even as a discontinuous layer.
C. Thick-walled cells present in pericyclic region though not necessarily conspicuous.
D. Resin canals marginal.....*A. grandis*
DD. Resin canals median.
E. Resin canals narrow, 1/4 to 1/3 as wide as leaf.....*A. Veitchii*
EE. Resin canals wide, 1/3 to 1/2 as wide as leaf.....*A. sachalinensis*
CC. Thick-walled cells absent from pericyclic region.
D. Resin canals marginal to sub-marginal.
E. Leaves not over 2 cm. long, pointed, rounded or emarginate at apices, revolute at margins.....*A. koreana*
EE. Leaves up to 6 cm. long, rounded or bifid at apices.....*A. grandis*
DD. Resin canals median to sub-marginal; some stomata frequently present on upper surface.
E. Leaves distinctly slender as far as fir leaves are concerned, many not over 1 mm. wide, and up to 3 cm. long.....*A. sibirica*
EE. Leaves usually at least 1.5 mm. wide and not over 2.5 cm. long.
F. Resin canals distinctly median; some stomata frequently present on upper surface.....*A. balsamea*
FF. Resin canals more or less submarginal; stomata absent from upper surface.....*A. Mariesii*
BB. Hypodermal layer present, continuous or discontinuous, at least along the upper surface and at lateral margins, sometimes extending to lower surface but never in immediate region of stomata.
C. Hypodermal layer more or less continuous, only an occasional cell or two lacking along upper surface.
D. Thick-walled cells absent from pericyclic region.
E. Leaves frequently stomatiferous on upper surface near apex.....*A. numidica*
EE. Leaves not stomatiferous on upper surface.....*A. amabilis*
DD. Thick-walled cells present in pericyclic region.
E. Leaves more or less revolute.
F. Leaves distinctly revolute appearing ω-shaped in cross-section.....*A. Delavayi*
FF. Leaves only moderately revolute.....*A. Forrestii*
EE. Leaves not revolute.
F. Thick-walled cells frequently present in chlorenchyma, not necessarily in every section.....*A. firma*

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[1] This species is usually regarded as a variety of *A. lasiocarpa* from which it differs, primarily, in possessing thick, corky, creamy-white bark.

FF. Thick-walled cells absent from chlorenchyma.
G. Resin canals median or sub-marginal.
H. Hypodermal-cells conspicuously thick-walled.
I. Leaves spiny pointed.....*A. holophylla*
II. Leaves blunt or bifid.....*A. homolepis*
HH. Hypodermal-cells moderately thick-walled.
I. Cross-sections showing more or less prominent broad midrib on lower surface, groove along upper surface and resin canals nearer margins than vascular bundle.....*A. Bornmülleriana*[3]
A. Borissi-regis
II. Cross-sections showing no prominent broad midrib along lower surface.
J. Resin canals distinctly median, equally distant from margins and vascular bundles; leaves half as thick as wide.....*A. squamata*
JJ. Resin canals median but tending to be nearer margins; leaves only one third as thick as wide and tapering toward margin.....*A. Fargesii*[4]
A. Faxoniana
GG. Resin canals marginal or sub-marginal.
H. Groove absent along upper surface resulting in straight upper margin of cross-sections; leaves spiny-pointed .....*A. venusta*
HH. More or less distinct groove present along upper surface; leaves sharp-pointed in some.
I. Lateral margins bluntly pointed.
J. Leaves up to 6 cm. long; epidermal and hypodermal cells quite similar in size and wall-thickness.....*A. spectabilis*
JJ. Leaves not over 3 1/2 cm. long; hypodermal cells more conspicuous than epidermal and generally thicker-walled.....*A. chensiensis*
II. Lateral margins more or less rounded.
J. Hypodermal layer frequently 2 or 3 cells thick, especially along lateral margins and midrib.
K. Leaves sharply pointed...*A. cephalonica*
KK. Leaves not sharply pointed..*A. cilicica*
JJ. Hypodermal layer usually one cell and only occasionally 2 or more cells thick.
K. Leaves sharply pointed or at least acute, bent backward along twig..*A. recurvata*
KK. Leaves usually not sharply pointed; never bent backward.
L. Leaves up to 6 cm. long.....
.....*A. Pindrow*[5]
A. spectabilis

[3] These two species differ chiefly in the presence of dense short pubescence on the branchlets of *A. Borisii-regis*.

[4] Of these two species only *A. Faxoniana* has branchlets which are densely pubescent.

LL. Leaves seldom over 3 cm. long.
M. Outer epidermal walls conspicuously thicker than inner or radial walls; lateral margins sometimes rounded, sometimes bluntly pointed resulting from increased number of closely packed hypodermal cells. . *A. Beissneriana*
MM. Outer epidermal walls moderately thicker than inner or radial ones; lateral margins always rounded.
N. Thick-walled cells in pericyclic region very conspicuous by virtue of their number and wall-thickness. . . *A. religiosa*
NN. Thick-walled cells in pericyclic region not especially conspicuous. . . . . *A. sutchuenensis*
CC. Hypodermal layer discontinuous; present, at least, in the center along both sides.
D. Thick-walled cells present in pericyclic region.
E. Resin canals median. . . . . *A. nephrolepis*
EE. Resin canals marginal.
F. Thick-walled cells strikingly abundant. . . . . *A. religiosa*
FF. Thick-walled cells few. . . . . *A. alba*
DD. Thick-walled cells absent from pericyclic region.
E. Resin canals marginal. . . . . *A. Nordmanniana*
EE. Resin canals median
F. [6]Leaves with 8–12 lines of stomata in each band. . . . *A. Fraseri*
FF. [6]Leaves with 4–8 lines of stomata in each band. . . . *A. balsamea*

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[5] *A. spectabilis* is distinguishable from *A. Pindrow* by its grooved branchlets and the presence of hairs in the grooves.
[6] Adapted from Rehder and verified.

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Explanation of plates 26–32

Fig. 1. *A. chensiensis* Van Tiegh., Bull. Soc. Bot. France **38:** 413 (1891): bluntly pointed lateral margin, marginal resin canal and moderately thick-walled hypodermal cells. China.

Fig. 2. *A. Veitchii* Lindl: median resin canal, absence of hypodermal layer and presence of stomata only on lower surface.

Fig. 3. *A. nephrolepis* Maxim: discontinuous hypoderm composed of moderately thick-walled cells.

Fig. 4. *A. firma* Sieb. & Zucc.: excessively thickened walls of hypodermal cells.

Fig. 5. *A. firma* Sieb. & Zucc.: two slightly separated vascular strands, excessively thick-walled cells in the pericyclic region within the endodermis and two such cells in the chlorenchyma outside the endodermis.

Fig. 6. *A. magnifica* Murr.: a region of the hypoderm composed of several rows of moderately thick-walled cells.

Fig. 7. *A. balsamea* Mill.: longitudinal section of leaf showing intercellular spaces in palisade parenchyma.

Fig. 8. *A. Nordmanniana* Spach: marginal resin canal and continuous hypoderm composed of one layer of moderately thick-walled cells.

Fig. 9. *A. nobilis* Lindl.: unseparated vascular strand.

Fig. 10. *A. balsamea* Mill.: two widely separated strands of vascular tissue and absence of thick-walled cells in pericyclic region.

Fig. 11. *A. homolepis* Sieb. & Zucc.: two separated vascular strands and abundant thick-walled cells in pericyclic region.

Fig. 12. *A. concolor* Lindl. & Gord., Jour. Hort. Soc. Lond. **5:** 210 (1850). Colorado to southern and Lower California, northern continental Mexico and New Mexico.

Fig. 13. *A. cilicica* Carr., Conif. 229 (1855). Asia Minor (Cilicia), northern Syria.

Fig. 14. *A. Veitchii* Lindl., Gard. Chron. 23 (1861). Mountains of central Japan.

Fig. 15. *A. grandis* Lindl., Penny Cyclop. **1:** 30 (1833). Vancouver Island to northern California, east to Montana, near the coast and in mountains.

Fig. 16. *A. Pinsapo* Boiss., Bibl. Univ. Genève **13:** 167 (1838). Southern Spain.

Fig. 17. *A. Nordmanniana* Spach, Hist. Veg. Phan. **11:** 418 (1842). Caucasus, Asia Minor, Greece.

Fig. 18. *A. Faxoniana* Rehd. & Wils., Sargent, Pl. Wils. **2:** 42 (1914). High altitude forests in western China.

Fig. 19. *A. Pindrow* Spach, Hist. Veg. Phan. **11:** 423 (1842). Western Himalaya, Kumaon to Kashmir.

Fig. 20. *A. nephrolepis* Maxim., Bull. Acad. Petersb. **10:** 486 (1866). Eastern Siberia, northern China.

Fig. 21. *A. spectabilis* Spach., Hist. Veg. Phan. **11:** 422 (1842). Sikkim and Bhutan Himalaya.

Fig. 22. *A. Forrestii* Craib, Notes Bot. Gard. Edin. **11:** 279 (1920). Southwestern China at high altitudes.

Fig. 23. *A. Mariesii* Mast., Gard. Chron. **12:** 789 (1879). Mountains of Japan.

Fig. 24. *A. sachalinensis* Mast., Gard. Chron. **12:** 588 (1879). Northern Japan, Saghalin and Kurile Islands.

Fig. 25. *A. squamata* Mast., Gard. Chron. **39:** 299 (1906). Western China at high altitudes.

Fig. 26. *A. homolepis* Sieb. & Zucc., Fl. Jap. **2:** 17 (1842). Mountains of Japan.

Fig. 27. *A. venusta* K. Koch, Dendrol. **2** II: 210 (1873). Monterey County, California, at elevations of about 3000 feet.

Fig. 28. *A. cephalonica* Loud., Gard. Mag. **14:** 81 (1838). Mountains of Greece.

Fig. 29. *A. recurvata* Mast., Jour. Linn. Soc. Bot. **39:** 299 (1906). Western China.

Fig. 30. *A. sibirica* Ledeb., Fl. Alt. **4:** 202 (1833). Northern Russia to Kamchatka, Altai Mountains, south to Turkestan and Manchuria.

Fig. 31. *A. arizonica* Merr., Proc. Biol. Soc. Washington **10:** 116 (1896). Northern Arizona and northern New Mexico, southern Colorado.

Fig. 32. *A. Delavayi* Franch., Jour. de Bot. **13:** 258 (1899). Western China at high altitudes.

Fig. 33. *A. nobilis* Lindl., Penny Cyclop. **1:** 30 (1833). Washington to northern California.

Fig. 34. *A. holophylla* Maxim., Bull. Acad. Petersb. **10:** 487. 1866. Manchuria and Korea.

Fig. 35. *A. firma* Sieb. & Zucc. Fl. Jap. ii 15t. 107 (1842). Japan up to 7000 feet elevation.

Fig. 36. *A. sutchuenensis* Rehd. & Wils. Sargent, Pl. Wils. **2:** 48 (1914). Western China.

Fig. 37. *A. koreana* Wils., Jour. Arn. Arb. **1:** 188 (1920). Mountains of Korea.

Fig. 38. *A. balsamea* Mill. Gard. Dict. ed. 8 n. 3 (1768). Labrador to West Virginia, west to Minnesota and Iowa.

Fig. 39. *A. lasiocarpa* Nutt. North American Sylva **3:** 138 (1849). Alaska to Oregon, Utah and northern New Mexico.

Fig. 40. *A. alba* Mill. Gard. Dict. ed. 8. (1768). Mountains of central and southern Europe.

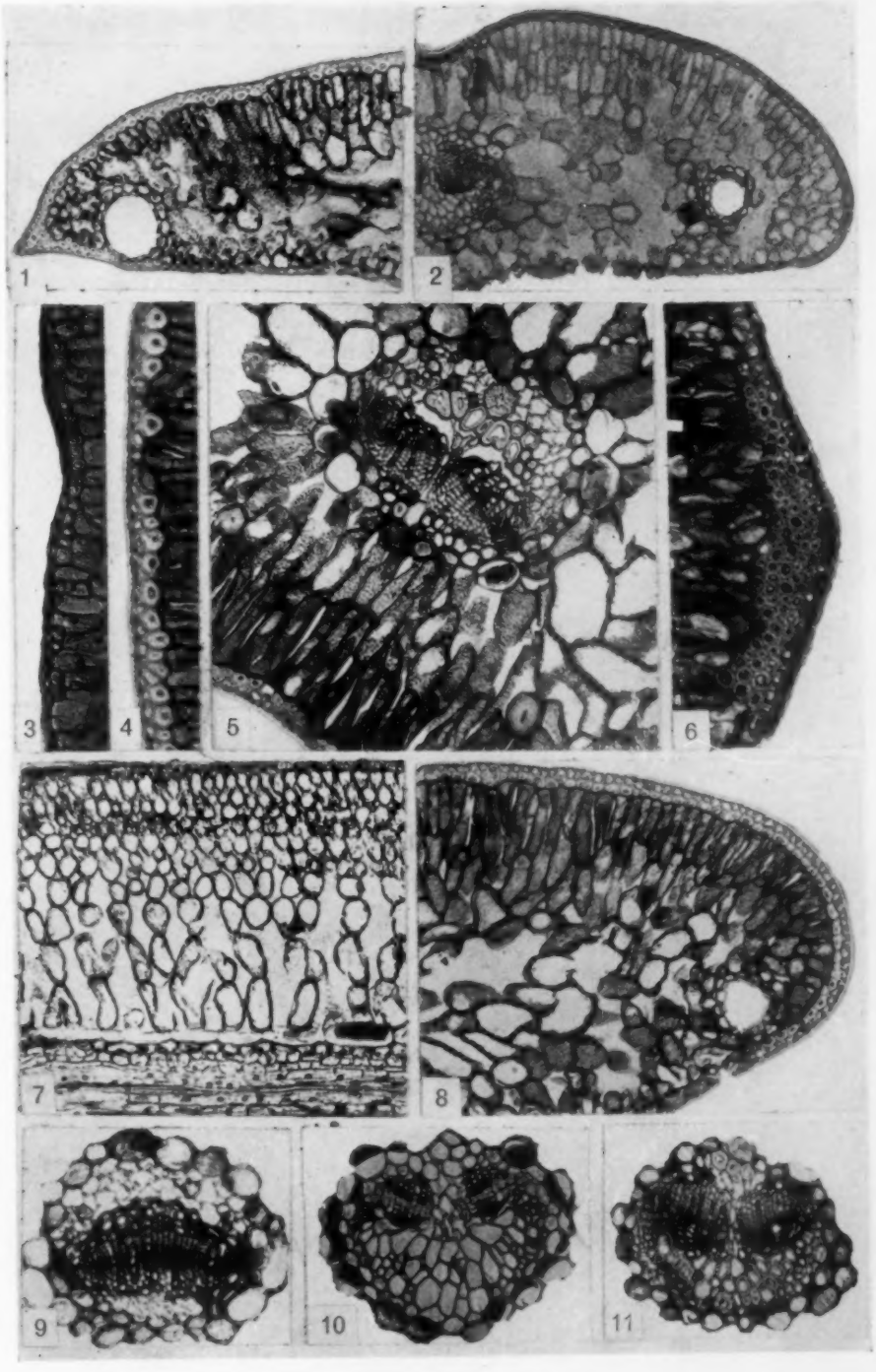
Fig. 41. *A. Fraseri* Poir., Lamarck Encyc. Method. Sup. v (1817). Alleghany Mountains, West Virginia to North Carolina and Tennessee.

Fig. 42. *A. magnifica* Murr., Proc. Roy. Hort. Soc. **3:** 318 (1863). Oregon to California, 5000 to 10,000 feet elevation.

Fig. 43. *A. amabilis* Forb., Pin. Wob. 125 (1839). British Columbia and Alberta to Oregon.

Figures 1 to 11 represent magnifications of 75 to 100 diameters; all the others are about 50.

Photomicrographs of *A. Pindrow* and *A. spectabilis* are not typical of the species, being probably from fertile branches. On sterile branches, resin canals are normally marginal.



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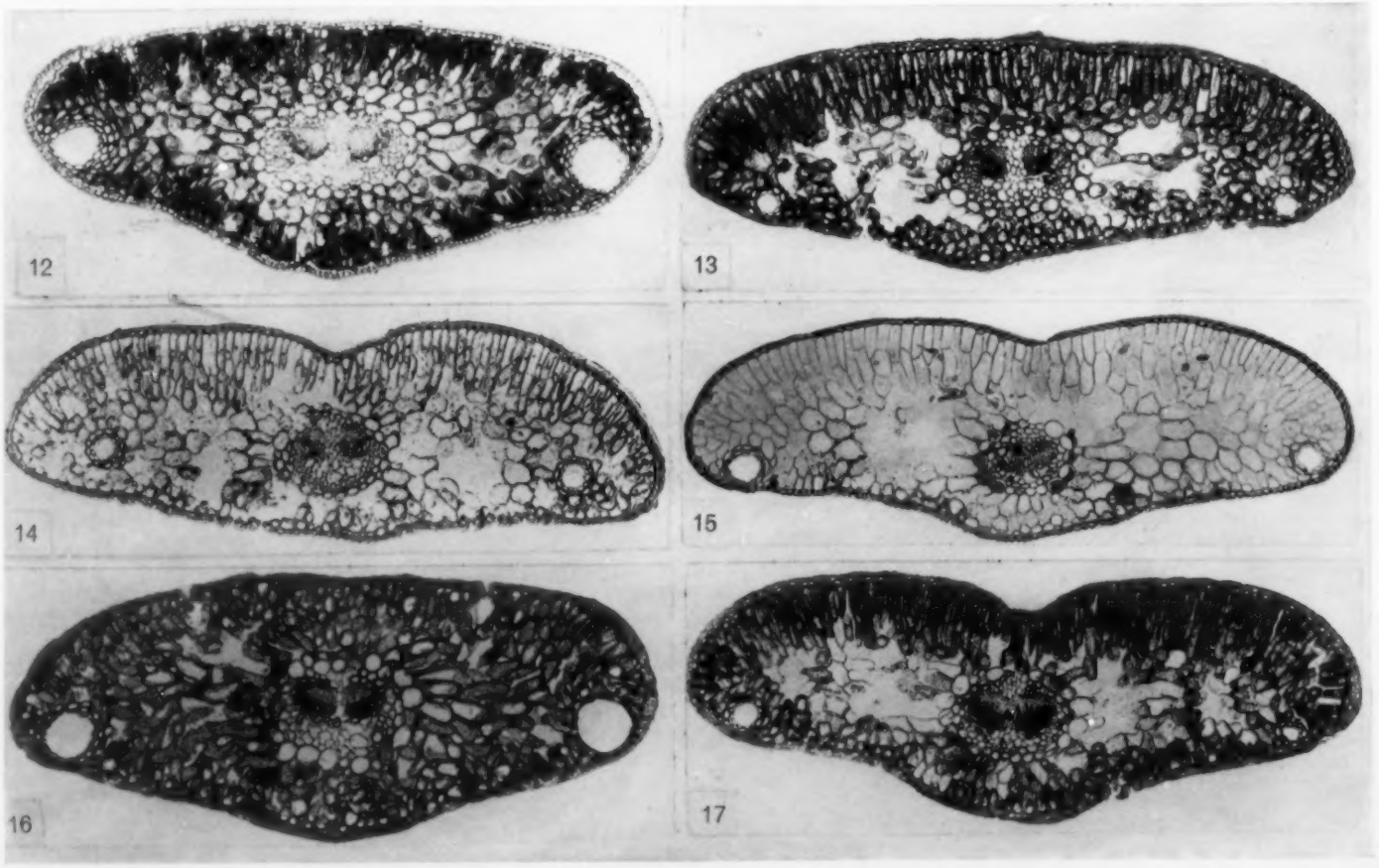

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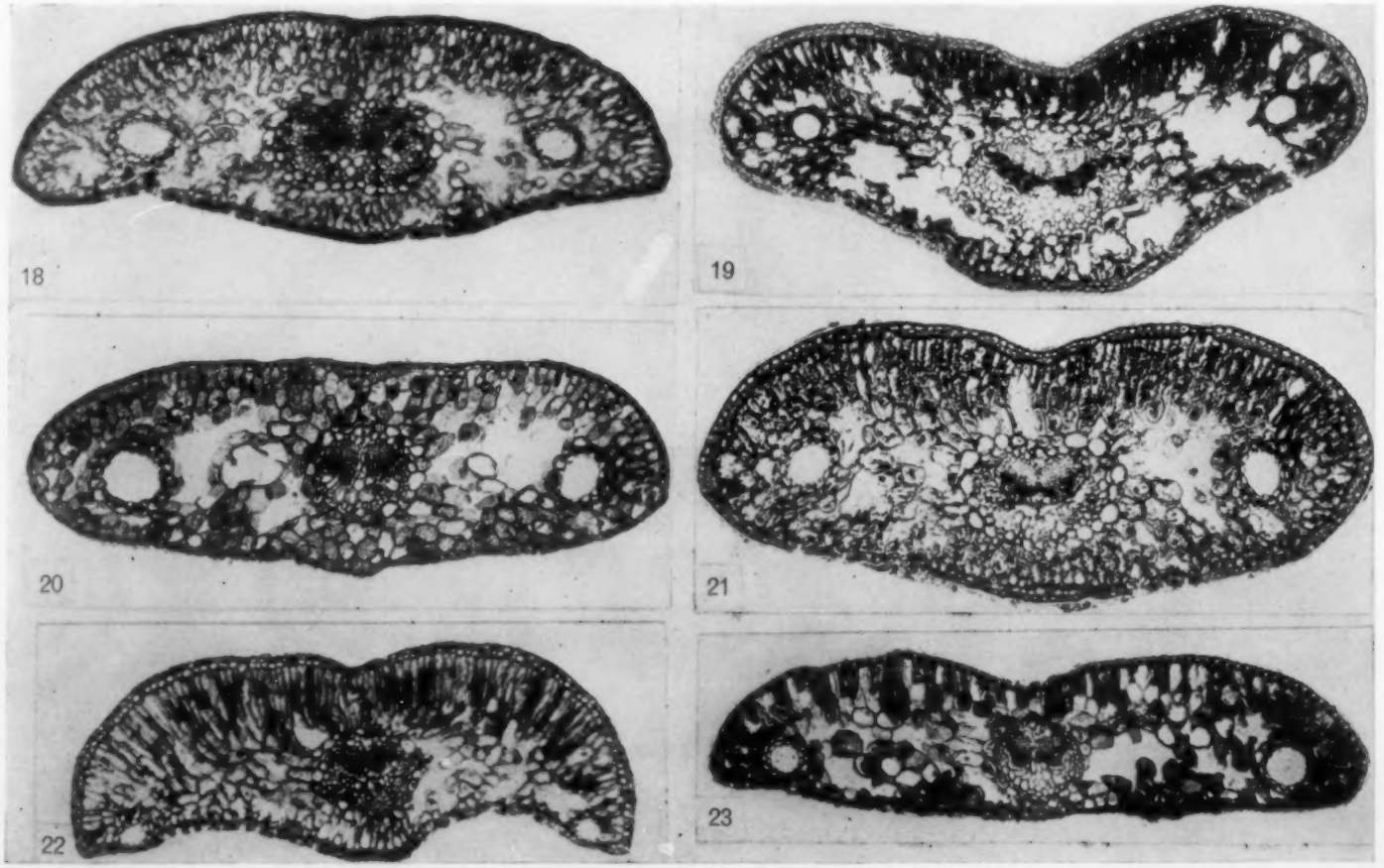

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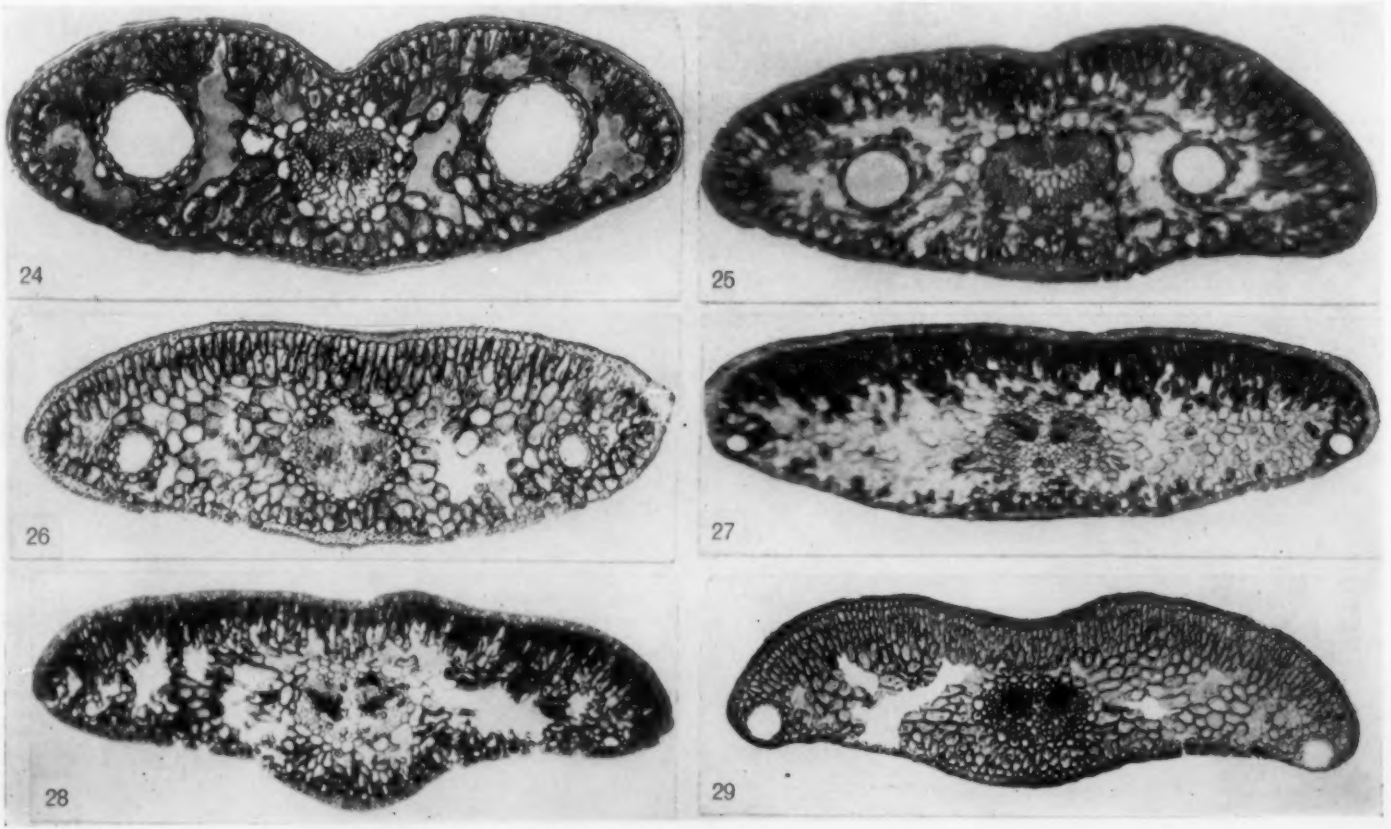

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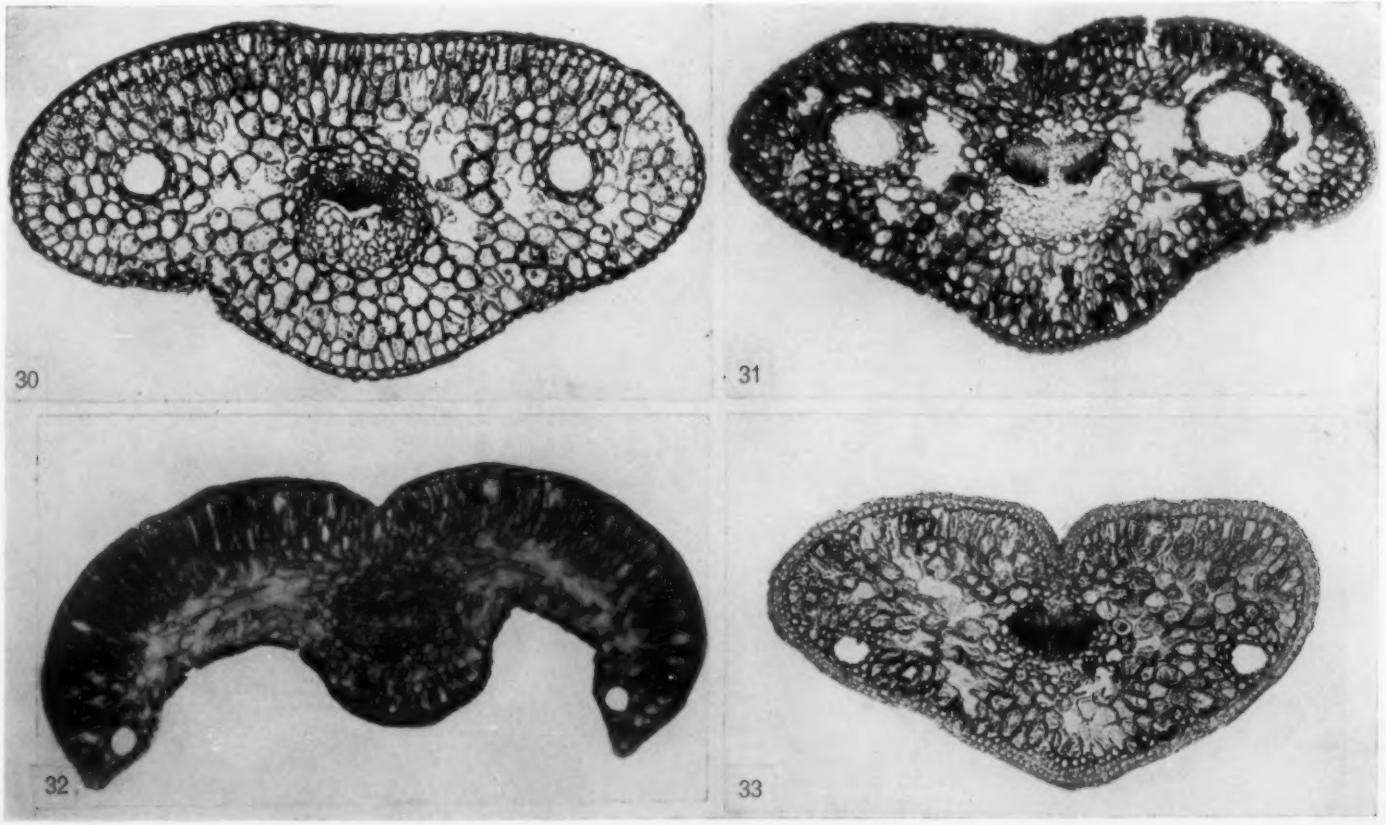

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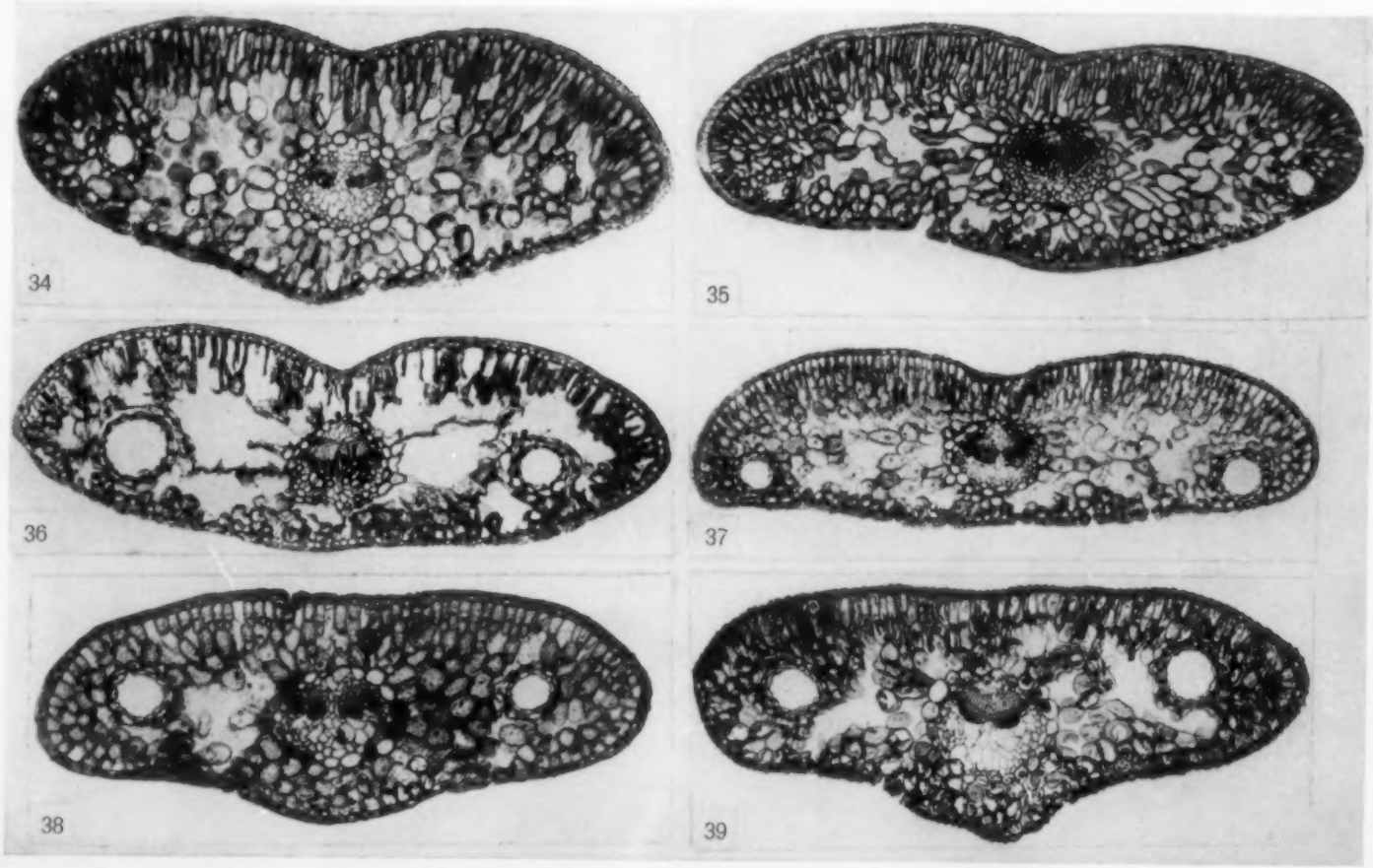

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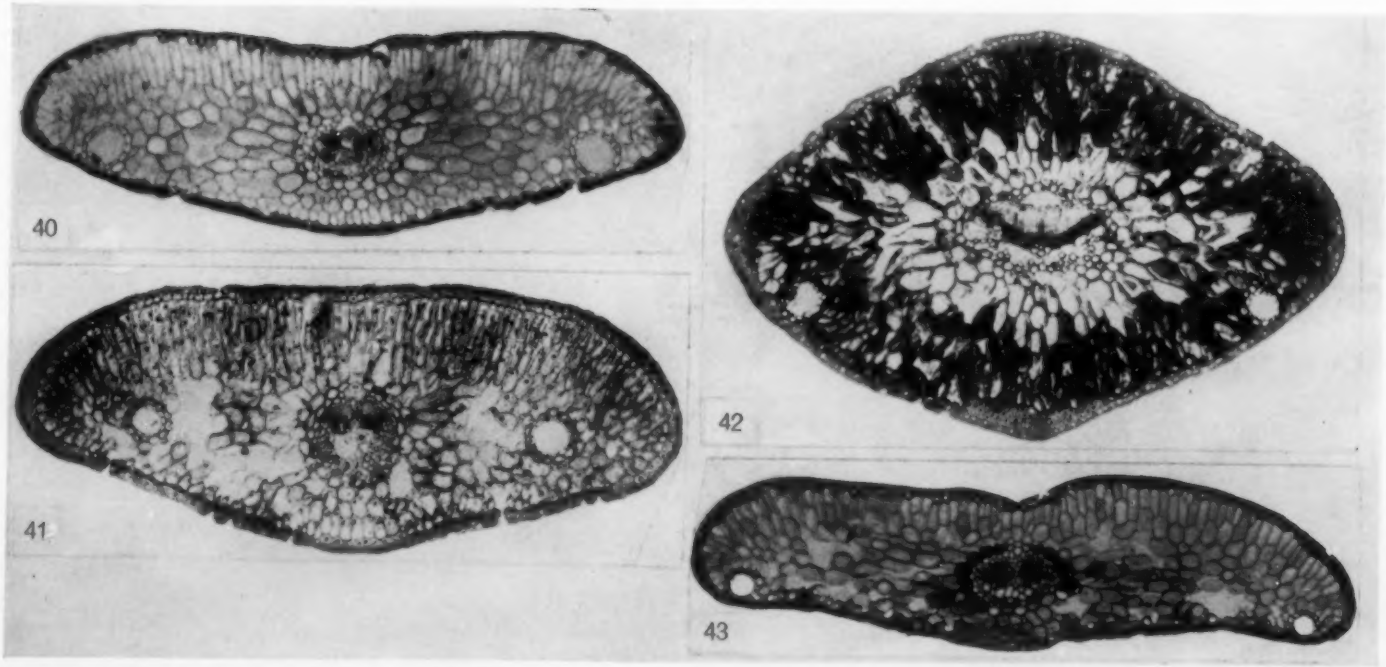

FULLING: LEAF STRUCTURE OF ABIES

UNIV. OF ILLINOIS

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1934

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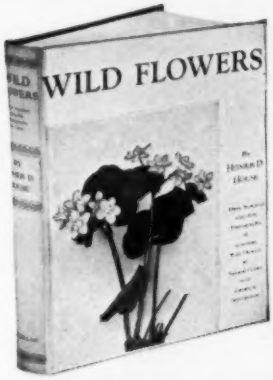

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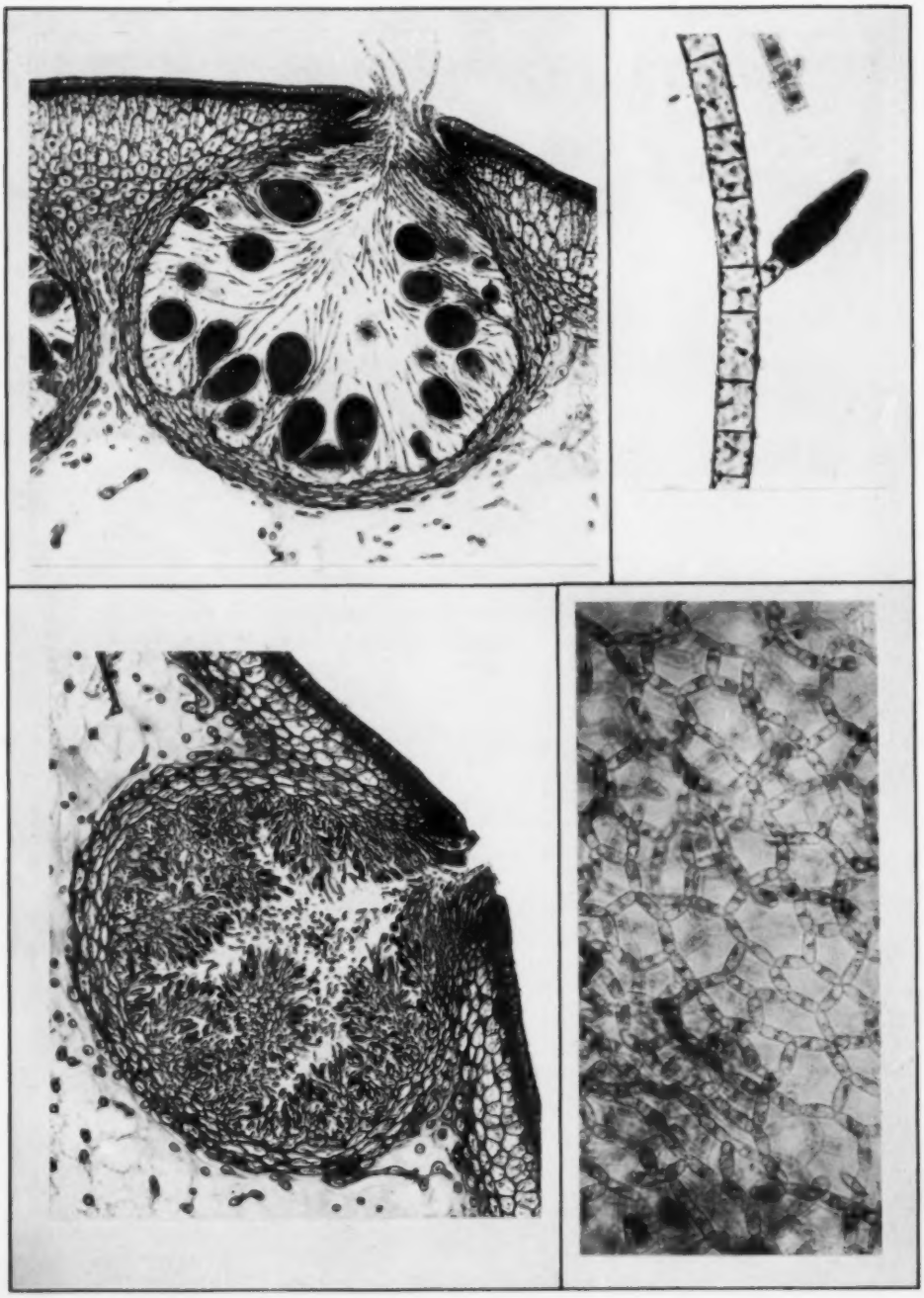

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